# MECHANISMS AND DEMOGRAPHIC CONSEQUENCES OF DISPERSAL IN THE COOPERATIVELY BREEDING MEERKAT

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**Dissertation**

zur

**Erlangung der naturwissenschaftlichen Doktorwürde**
**(Dr. sc. nat.)**

vorgelegt der

**Mathematisch-naturwissenschaftlichen Fakultät**

der

**Universität Zürich**

von

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**Zürich, 2019**

# TABLE OF CONTENTS

# SUMMARY

Dispersal is a key ecological process that influences the dynamics of spatially and socially structured populations through the maintenance of gene flow and recolonization of extinct habitat patches. Despite our appreciation of the importance of the process, we lack a firm empirical understanding of how dispersal is affected by social and environmental factors, and how it affects the overall dynamics of socially structured populations. Such lack of a thorough understanding of dispersal is due mostly to the difficulty of pursuing wide-ranging individuals of wild populations. In my thesis, I collected detailed life-history and movement data from dispersing female meerkats to gain a mechanistic understanding of dispersal in a cooperatively breeding species: that is, to assess the influence of individual, social, and environmental factors on each stage of dispersal and on the formation and demography of new groups.

In *Chapter Two*, I describe how individual, social, and environmental factors influence the transitioning between each stage of dispersal, dispersal distance, and dispersal time. I show a nonlinear relationship between population density and dispersal – i.e., daily emigration and settlement probabilities. Both are highest at low and high population densities, and lowest at medium densities. In addition, dispersal time increases with population density. I propose that limited benefits of cooperation at low population densities and increased kin competition at high densities are the causes for the observed nonlinear density effect.

In *Chapter Three*, I assess changes in body mass and stress hormone levels of dispersers in response to unfamiliar habitat and changing social environment. While previous studies have generally focused on the early stages of dispersal or on pre-dispersal exploratory movements, I describe the changes of body condition throughout the entire dispersal process and show that dispersers lose body mass and have increased stress hormone levels. My study provides empirical support for the theoretical predictions suggesting that changing physical and social environment during dispersal affect individuals' condition.

In *Chapter Four*, which is a supervised work, my students and I examine variation in defecation and urination probabilities during the consecutive stages of dispersal and discuss the secondary role of faeces and urine as scent marks for mate finding and territory establishment. Our analysis suggests that females use faeces as long-lasting signals to secure an exclusive territory during the settlement stage and urine as short-term within-coalition signals to advertise reproductive status to males, independent of dispersal stage.

In *Chapter Five*, I investigate the demography of newly settled disperser groups. I show that reproductive skew in new disperser groups is lower than in established resident groups, where reproduction is almost entirely monopolized by dominant females. My results suggest that dispersing subordinates have higher reproductive output than philopatric subordinates to compensate for the high costs associated with dispersal. By increasing their reproductive output, dispersers may be able to promote fast group augmentation and increase recolonization success.

In *Chapter Six*, I present a unique case of delayed post-implantation embryonic development in pregnant dispersing meerkats. Delayed embryonic development is very rare and has only been observed in a few bat species. It decouples implantation from parturition and gives an animal flexibility to time birth and lactation to favourable conditions. In dispersing meerkats, being able to delay parturition until a new territory is found can increase the survival of the first litter and the augmentation of the new group.

In conclusion, my study shows that different individual, social, and environmental factors affect dispersal decision and dispersers' body condition during consecutive stages of dispersal. This underlines the importance of studying drivers specific to each stage of dispersal and answers the call for empirical studies to test theoretical predictions. I further show that dispersers increase their potential to recolonise empty habitat patches through increased reproductive rates. As such, my thesis is a first step towards a comprehensive understanding of dispersal and new group formation in spatially and socially structured populations. My

findings, together with existing knowledge on resident-group processes, builds the foundation to assess the population-level consequences of dispersal. In the face of rapid environmental changes, including habitat loss and fragmentation, a better understanding of the dispersal process will improve our understanding of the dynamics and persistence of spatially and socially structured populations.

# CHAPTER ONE

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## General Introduction

# GENERAL INTRODUCTION

## Dispersal and population dynamics

Dispersal is a complex process that can strongly affect population dynamics at the local and broad spatial scales and plays a key role in linking spatially and socially structured populations (Bowler and Benton 2005, Clobert et al. 2009). It maintains gene flow among and genetic variability within existing populations (Lowe and Allendorf 2010), can prevent local populations from extinction, and recolonization of empty habitats can compensate for the extinction of local populations (Hanski 1999). Dispersal is typically divided into three subsequent stages – emigration from the natal group, transience through unfamiliar landscape, and immigration or settlement in a new territory – and each stage depends on different individual, social and environmental factors (Bowler and Benton 2005, Clobert et al. 2012). For instance, the decision of an individual to continue its dispersal endeavour versus returning to its natal group may depend upon changing social circumstances, such as the composition of its dispersing coalition, the social landscape represented by the distribution of conspecifics, and the successful encounter of potential mates with whom to establish a new group (Mares et al. 2014, Cozzi et al. 2018). Despite the ecological and evolutionary importance of dispersal, our models of socially and spatially structured populations often fail to incorporate its true complexity, and thus fail to accurately describe the dynamics of the overall system (Morales et al. 2010, Travis et al. 2012).

Dispersal can be regarded as the physical movement of individuals on a fitness landscape, and the high costs associated with each stage of dispersal are likely to induce strong selective pressures on dispersers' survival and reproduction (Bonte et al. 2012). Dispersing individuals are expected to adopt different dispersal strategies in response to changing physiological, social and environmental perturbations (e.g., kin competition, food availability), and these strategies ultimately determine their fitness (Nathan et al. 2008, Morales et al. 2010). Environmental

variables (e.g., food availability, climatic conditions) further influence individual conditions and hence distance travelled, time spent dispersing, survival rate, and settlement success (Bonte et al. 2012). Due to the intrinsic difficulty of following far-ranging individuals through space and time under natural conditions, however, dispersal and its determinants still remain relatively poorly understood (Tomkiewicz et al. 2010). Only in recent years, advances in GPS, battery life-time, data-retrieval technologies, and miniaturization of the components have allowed collection of high-resolution movement data over extended periods of time and from a variety of taxa (Cant et al. 2005, Schick et al. 2008, Singh et al. 2012); furthermore, advanced spatially-explicit models have contributed to accurately investigating previously unknown processes (Delgado et al. 2010, Rémy et al. 2011, Tarwater and Beissinger 2012, Debeffe et al. 2012). By following the fate of dispersing individuals, the empirical investigation of dispersal mechanisms and parameterization of survival and reproductive success – key fitness components – will be possible, thus adding a new, unexplored dimension to our understanding of life-history strategies and population dynamics.

**Dispersal in social species**

Population dynamics of group-living, social species are determined by within- and between-group dynamics, where the formation of new groups depends on the survival and reproduction of dispersing individuals (Bjørnstad et al. 1999). In social species, dispersal is performed by non-breeding subordinate helpers (Clutton-Brock 2002, Koenig and Dickinson 2004) who play a key role in the persistence of these populations, especially if local extinctions and colonisations are prevalent (Hanski 1999). Mainly due to practical limitations and the difficulty of monitoring far-ranging individuals, however, inferences about population dynamics processes have traditionally been drawn on few established social groups and have ignored dispersal events (Ozgul et al. 2009, Bateman et al. 2013). These shortcomings often lead to assumptions that underestimate the survival and breeding of subordinate dispersers, and consequently their contribution to average population fitness (Koenig et al. 1996, Cooper et al.

2008). To gain a comprehensive and spatially-explicit understanding of social breeder dynamics, long-term life-history data of both dispersers and residents are needed (Belchion 1996).

In some social species – occurring in insects, birds, and mammals – a single female in each group monopolizes reproduction and her offspring is reared by several subordinate helpers (Clutton-Brock 2009). In these cooperatively breeding species, subordinates attain indirect fitness benefits by raising closely related siblings (Koenig and Dickinson 2004). Although subordinate helpers of some cooperative species can occasionally breed in their natal group, they must disperse and form new groups to increase their direct fitness through independent reproduction (Keller and Reeve 1994). Due to high costs associated with dispersal, however, subordinates often delay dispersal and remain in the natal group where they profit from the benefits of group-living (Koenig et al. 1992, Kokko and Ekman 2002). Depending on social circumstances and environmental conditions, individuals will either remain at home and help raising their siblings or disperse and form their own breeding unit. For instance, the decision to disperse may be promoted by low population densities in the natal area, as the benefits of cooperation decrease with decreasing number of helpers (Hoogland 2013); but the prospects of finding vacant territories elsewhere increase as resident groups become smaller or go extinct (Lambin et al. 2001, Kokko and Lundberg 2001). To understand the population-level consequences of dispersal in cooperative breeders, we must investigate how the fitness trade-off between philopatry and dispersal relates to individuals' social and physical environment.

In my thesis, I investigate the dispersal of subordinate females in a wild population of a cooperatively breeding species. The aim of my study is to provide detailed information on dispersal propensity and the transitioning of subordinate females through the three stages of dispersal; to assess the morphological and physiological costs associated with dispersal; to examine the behavioural aspects of settlement and new group formation; and to investigate the

demography of new groups for several years. As such, my work provides a more mechanistic description of the dispersal process than previous studies. Combined with already existing life-history data on within-group processes, my thesis builds the foundation to assess alternative life-history strategies and will contribute to our understanding of the demographic and evolutionary consequences of dispersal in socially and spatially structured populations.

**Study system**

Meerkats (*Suricata suricatta*) are cooperatively breeding mongooses that live in groups of up to 50 individuals and are well suited to investigate dispersal in social species. Groups are characterized by a dominant pair that monopolizes the majority of the group's reproduction and several subordinate helpers that delay dispersal and help rearing their younger siblings (Clutton-Brock et al. 1999, Griffin et al. 2003). While subordinate meerkats gain indirect fitness through kin selection in their natal group and profit from cooperative benefits of living in a large group, they have to disperse and incur the costs of moving through unknown habitat to increase their direct fitness (Clutton-Brock and Manser 2016). Both males and females disperse in same-sex multiple member dispersing coalitions which may alleviate some of the costs associated with dispersal (Young 2004); for instance, large coalitions may profit from increased competitive abilities when encountering conspecifics or from improved reproduction by initiating a new group with several helpers. However, because males and females are characterized by different investments into reproductive effort and parental care, subordinate individuals of the two sexes may adopt different dispersal strategies that maximise their fitness.

Sexually mature subordinate males repeatedly conduct short extra-territorial forays during which they achieve extra-group paternity (Young et al. 2005, 2007). Subordinate males may meet future dispersing partners during such forays or immigrate into and take over a foreign group (Mares et al. 2014). On the contrary, dispersal is only beneficial for females by establishing a new group upon successful settlement in a new territory – immigration and group

takeover by females has never been documented in meerkats. The limited likelihood of successfully increasing their own direct fitness through dispersal may explain why female meerkats are reluctant to leave their natal group and do so only when aggressively evicted by the dominant female (Young et al. 2006, Clutton-Brock et al. 2008). As female dispersal is restricted to settlement and new group formation, its success is likely to depend on different factors than those affecting male dispersal and can be expected to be very costly.

**Study population and area**

I conducted my study in the South African Kalahari Desert between September 2013 and July 2018. The study area was located on the Kuruman River Reserve (26° 59' S, 21° 50' E) and the surrounding ranch land, 20 km south of the Botswana border (Figure 1a). I had access to habituated study animals and research facilities that have been maintained by the Kalahari Meerkat Project (KMP) for the past 20 years. This provided me with the unique opportunity to collect high-resolution movement and long-term life-history data on female dispersers at an unprecedented level of detail. Furthermore, I could compare dispersers to their resident counterparts because information on within-group dynamics was already available (Bateman et al. 2013, Ozgul et al. 2014). The core study area was located along the fossil bed of the Kuruman river and the adjacent sparsely vegetated sand dunes and intermittent saltpans. Subordinate females were evicted and dispersed from their natal groups mainly during the breeding season between October and April when most of the annual rainfall occurs (Clutton-Brock et al. 2008). The region is further characterised by large daily and seasonal temperature variations with hot summers (October-April) and cool winters (May-September, Clutton-Brock et al. 1998a).

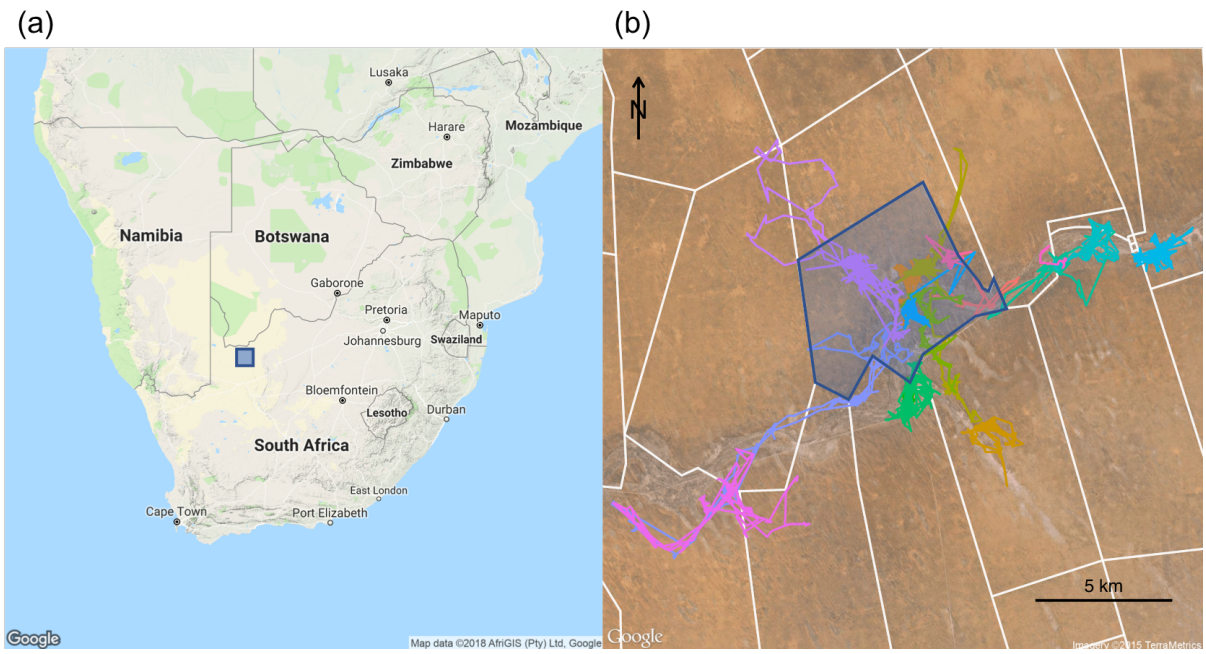


*Figure 1. a) Location of the study site (blue box) in the southern Kalahari Desert. b) Movement trajectory examples of dispersing female meerkats leading from the Kuruman River Reserve (blue polygon) to the surrounding ranch land (white lines mark ranch borders).*

**General methods**

The eviction of subordinate female meerkats by the dominant female is usually preceded by increasing levels of aggression from the dominant female and, hence, eviction events can be anticipated (Clutton-Brock et al. 1998a). Therefore, I was able to capture and collar subordinate females a few days prior or immediately after eviction from their natal group. The collars were composed of a VHF module (Holohil Systems, Carp, Ontario, Canada) and a GPS module (CDD, Athens, Greece), and weighed a total of 25 g (~ 3.5 % of meerkat body mass). Collars of this size and weight do not affect meerkat behaviour and survival (Golabek et al. 2008), and I did not observe any sign of distress in animals carrying collars. Typically, only one individual in each dispersing coalition was fitted with a radio-collar. To mount the collars, we sedated individuals using a mixture of isoflurane and oxygen (Figure 2a) in compliance with the KMP protocol and in collaboration with trained project staff (Jordan et al. 2007). All

necessary permits to handle and tag meerkats were granted to the KMP by the Department of Environment and Nature Conservation of South Africa and the Animal Ethics Committee of the University of Pretoria (permit "FAUNA 192/2014"). I used GPS locations to identify time of emigration and time of settlement, and to calculate movement measures such as dispersal distance and dispersal time (see *Chapter Two* for more details).

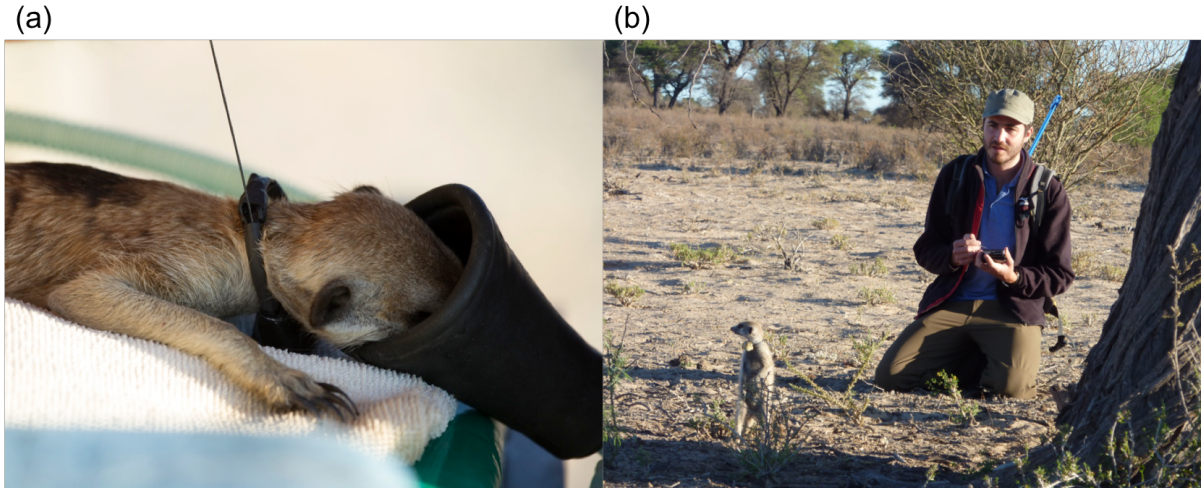


*Figure 2. a) Anaesthetised meerkat is equipped with a GPS radio-collar using a mixture of isoflurane and oxygen. b) Data collection in the field.*

I systematically followed the fate of both short- and long-distance dispersers that moved up to 12 km beyond the main study area (Figure 1b), which corresponds to more than 7 times the width of an average meerkat home range. I located collared dispersing female coalitions by means of VHF radio-tracking every two to seven days. Study animals were part of the long-term research at the KMP and were habituated to the presence of humans and trained to step on a portable weighing scale (Clutton-Brock et al. 1998b). Hence, at each visit, I was able to record data on dispersing coalition size, number of associated unrelated males from other groups, and pregnancy status; and I measured individual body mass and collected faecal samples for stress hormone metabolite analysis (see *Chapter Three* for more details). I further recorded individual behaviours such as marking and dominance interactions from close proximity (Figure 2b, *Chapter Four*); and I was able to estimate survival and reproductive rates

at an almost daily basis (*Chapter Five*). Data on individual age, relatedness, natal group composition, and population density were available from the long-term database of the KMP; and rainfall and temperature were measured with an on-site weather station.

**Thesis objective and outline**

The chapters of my thesis are organized as self-contained manuscripts that have been or will be submitted to peer-reviewed journals. This inevitably leads to some overlap among the chapters, especially in the methods section of each manuscript. Specifically, my thesis contains the following six chapters:

In *Chapter Two*, I describe in detail how individual, social, and environmental factors influence the probability for an individual to transition from one dispersal stage to the next; and how dispersal distance and dispersal time are affected by the same factors. Using data from 65 dispersing female coalitions, I show that there is a nonlinear relationship between population density and daily emigration and settlement probabilities, being highest at low and high population densities, and lowest at medium densities. My study is one among few to show nonlinear density-dependent dispersal in wild animals and the first to describe it throughout the whole dispersal process. In cooperative breeders, limited benefits of cooperation at low population densities and increased kin competition at high densities are likely explanations for inverse density effects.

In *Chapter Three*, I compare changes in body mass and stress hormone output of dispersers that successfully settle to those of females that return to their natal group after being away for a short period. While previous studies have generally focused on the early stages of dispersal or on pre-dispersal exploratory movements (Larsen and Boutin 1994, Young et al. 2006, Ridley et al. 2008), I extend existing knowledge by showing that successful dispersers lose more body mass and have higher stress hormone output than returning females. In addition, I show that stress hormone output increases during transience compared to the

emigration stage. This emphasises that dispersal through unfamiliar habitat is a costly process, but also suggests that conclusions regarding successful dispersal should be drawn very carefully when based only on prospecting individuals.

In *Chapter Four*, which is a supervised work, my students and I examine variation in defecation and urination probabilities during the consecutive stages of dispersal and discuss the usage of faeces and urine as scent marks for mate finding and territory establishment. To obtain rates of scent marking (i.e., defecation and urination events), we observed dispersing females for standardised time periods on several days and counted the number of marking events. To our knowledge, this is the first study showing changes in scent marking behaviour across all three stages of dispersal. Our investigation suggests that females use faeces as long-lasting signals to secure an exclusive territory during the settlement stage and urine as short-term within-coalition signals to advertise reproductive status to males, independent of dispersal stage.

In *Chapter Five*, I investigate the demography of dispersing females in newly settled groups and compare it to that of females in resident groups. I show that the reproduction of females in new disperser groups does not vary with social status and thereby increases the overall reproduction after settlement, whereas subordinate reproduction is almost entirely suppressed by dominant females in resident groups. My findings suggest that dispersers can promote fast group augmentation and recolonization success at the initial stages of group formation. This is a novel contribution as new group formation was thus far not observed in detail despite the general believe that dispersal-related processes have a large effect on the dynamics of spatially and socially structured populations (Bowler and Benton 2005). In addition, I provide empirical support for the prediction that dispersers should have higher fitness than philopatrics to compensate for the high costs associated with dispersal (Keller and Reeve 1994, Kokko and Ekman 2002). While philopatric female helpers attain only indirect

fitness through rearing close kin, dispersing subordinates can increase their direct fitness even if they do not attain the dominant position in the new group.

In *Chapter Six*, I present an observation unique to the reproductive cycle of meerkats. During my investigation of reproductive patterns in dispersers, I found that pregnant dispersing meerkats – which are forced out of their natal territory by aggressive evictions and travel through unfamiliar habitat – prolong their gestation by means of delayed post-implantation embryonic development. Delayed development is very rare and has only been observed in a few bat species (Orr and Zuk 2014). It decouples implantation from parturition and gives an animal flexibility to time birth and lactation to favourable conditions. In dispersing meerkats, it may be crucial to delay parturition until new habitat is found to ensure a first successful litter to augment the new group. In contrast to other species with variable gestation length, where delays are mostly caused by environmental factors such as temperature or spring conditions, delays in cooperative species may be a question of sociality, where social suppression could initiate the observed prolongation.

In *Chapter Seven*, the General Discussion, I summarise the main findings from the previous chapters to broaden the relevance of my study to dispersal and population dynamics in general. Identification of the factors influencing dispersal and associated fitness costs, and more realistic inclusion of movement into predictive population models will improve our understanding of how wildlife populations can prosper in the face of rapid environmental change. This is particularly important as the long-term persistence of populations in human dominated environments (e.g. habitat loss and fragmentation) in part depends on dispersing individuals that find conspecifics and suitable habitat to breed.

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# CHAPTER TWO

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## Density-dependent dispersal strategies in a cooperative breeder

*Ecology (2018) 99:1932–1941*


Photo credit: Arpat Ozgul

# Density-dependent dispersal strategies in a cooperative breeder

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**ABSTRACT**

Dispersal is a key ecological process that influences the dynamics of spatially and socially structured populations and consists of three stages – emigration, transience, and settlement – and each stage is influenced by different social, individual, and environmental factors. Despite our appreciation of the complexity of the process, we lack a firm empirical understanding of the mechanisms underlying the different stages. Here, using data from 65 GPS-collared dispersing female coalitions of the cooperatively breeding meerkat (*Suricata suricatta*), we present a comprehensive analysis of the effects of population density, mate availability, dispersing coalition size, and individual factors on each of the three stages of dispersal in a wild population. We expected a positive effect of density on dispersal due to increased kin competition at high densities. We further anticipated positive effects of mate availability, coalition size, and body condition on dispersal success. We observed increasing daily emigration and settlement probabilities at high population densities. In addition, we found that emigration and settlement probabilities also increased at low densities and were lowest at medium densities. Daily emigration and settlement probabilities increased with increasing female coalition size and in the presence of unrelated males. Furthermore, the time individuals spent in the transient stage increased with population density, whereas coalition size and presence of unrelated males decreased dispersal distance. The observed nonlinear relationship between dispersal and population density is likely due to limited benefits of cooperation at low population densities and increased kin competition at high densities. Our study provides empirical validation for the theoretical predictions that population density is an important factor driving the evolution of delayed dispersal and philopatry in cooperative breeders.

**Keywords:** Delayed dispersal, distance, dispersal stage, emigration, kin competition, meerkat, nonlinear dispersal, population density, settlement, transience

## INTRODUCTION

Dispersal of individuals is an important process regulating the persistence of populations as these populations depend on individuals that leave their natal patch, find suitable breeding habitat, and reproduce (Bowler and Benton 2005). Dispersal is typically divided into three stages: emigration from the natal group, transience through unfamiliar landscape, and settlement in a suitable habitat, and the outcome of a dispersal event depends on the decisions that dispersers take at each stage (Bowler and Benton 2005, Clobert et al. 2009). Nonetheless, existing theory often makes oversimplifying assumptions about dispersal and does not account for all three stages. Empirical data are particularly scarce for the transient and settlement stages due to the difficulty of following wide-ranging individuals under natural conditions (Tomkiewicz et al. 2010). In recent years, technological progress in animal tracking has allowed systematic collection of dispersal data (Cant et al. 2005, Schick et al. 2008, Singh et al. 2012), and advanced spatially explicit models have revealed previously unknown processes (Delgado et al. 2010, Remy et al. 2011, Debeffe et al. 2012, Tarwater and Beissinger 2012, Travis et al. 2012). However, our current knowledge of dispersal does not entirely capture the overall complexity, and more comprehensive empirical investigations of underlying mechanisms are needed (Bowler and Benton 2005, Clobert et al. 2009).

Among others, population density, resource availability, and inbreeding avoidance have been proposed to influence dispersal of individuals and the transitioning between dispersal stages (Bonte et al. 2012, Travis et al. 2012). Population density can have positive or negative effects on the rate of emigration depending on several circumstances (Bowler and Benton 2005, Matthysen 2005). For instance, high densities in the natal area can reduce fitness due to increased resource competition and aggression among conspecifics (Bowler and Benton 2005), leading to a positive relationship between population density and emigration. At the opposite end, negative density-dependent dispersal can arise when high density is associated with high-quality habitat at the natal patch (Baguette et al. 2011) or when resources are unevenly

distributed across space (McPeek and Holt 1992). Finally, a nonlinear relationship between population density and dispersal is expected where individuals emigrate at low population densities to avoid Alee effects (e.g., inbreeding, lack of breeding partners), remain in the natal area when densities increase and mates become more abundant, and disperse at very high densities when competition for resources intensifies (Courchamp et al. 1999, Loe et al. 2009, Shaw and Kokko 2014).

Density-mediated dispersal in social species is characterized by an additional level of complexity due to cooperation among group members. In these species, emigration can be negatively density dependent (Kokko and Lundberg 2001, Matthysen 2005) if the benefit of group living exceeds the cost of kin competition (Clutton-Brock 2002). At very low population densities, the benefits of cooperation decrease and individuals are more likely to disperse (Clutton-Brock and Lukas 2012, Hoogland 2013). However, this relationship is not always clear as competition at the natal site can decrease the inclusive fitness among kin (Hamilton and May 1977). Kin competition is, therefore, predicted to induce dispersal and several empirical studies support this prediction (Moore et al. 2006, Cote et al. 2007). In cases where kin competition outweighs the benefits of cooperation, population density is expected to have a positive effect on emigration. During transience, population density often has a negative effect on dispersal as saturated habitats increase the probability of aggressive encounters with conspecifics and decrease the likelihood of finding vacant territory (Kokko and Lundberg 2001, Lambin et al. 2001, Morton et al. 2018).

Several other intrinsic and extrinsic factors can be expected to influence the fate of a dispersal event. Larger individuals or individuals in better condition often have an advantage during transience and dispersal distance often increases with body mass (Barbraud et al. 2003, Jenkins et al. 2007, del Delgado et al. 2010, Debeffe et al. 2012). Individuals may move outside the range where relatives are found to avoid inbreeding (Long et al. 2008, Nelson-Flower et al. 2012), and the decision to settle in new territory is likely to be affected by the distribution of

unrelated mates (Davidian et al. 2016). Social species may be able to overcome ecological constraints during dispersal by forming multiple-member dispersing coalitions (Brown et al. 1982, Courchamp et al. 2000, Clutton-Brock et al. 2001). Individuals in larger coalitions are predicted to experience reduced predation risk (Clutton-Brock et al. 1999, Courchamp et al. 2000) and have increased competitive ability (Packer et al. 1990, Wilson et al. 2002, Young 2004). Environmental factors can further affect dispersal patterns. For instance, low rainfall has been suggested to promote delayed dispersal as poorer body condition can inhibit dispersal and independent reproduction (Molteno and Bennett 2006).

Meerkats (*Suricata suricatta*) are cooperative breeders and thus well suited to simultaneously investigate the effects of social, individual, and environmental factors on dispersal. Meerkats live in groups of 2–50 individuals, and groups are characterized by the presence of a dominant pair that monopolizes reproduction (Clutton-Brock et al. 2008). During her pregnancy, the dominant female often evicts one or multiple subordinate females (Young et al. 2006). Spontaneous female emigration is not observed, and eviction is the main mechanism promoting dispersal (Clutton-Brock et al. 1998a). Age, body mass, and pregnancy status of subordinates promote their eviction (Clutton-Brock et al. 2008, Ozgul et al. 2014), and when two or more females are evicted simultaneously, they form same-sex multiple-member coalitions (Clutton-Brock et al. 1998a). Hereafter, we will use the term "dispersing unit" to indicate both multiple-member coalitions and individuals that disperse alone. After eviction, females remain within the territory of the natal group for a variable period (hereafter, referred to as "post-eviction phase"; Fig. 1). At the end of this period, they are either accepted back to the natal group (hereafter, referred to as "returners"), or permanently emigrate and enter transience (hereafter, referred to as "emigrants"; Fig. 1). Previous work has shown a positive relationship between emigration and natal group size (Ozgul et al. 2014) and we therefore expect density to play a key role throughout dispersal.

The aim of this study was to investigate how social (population density, mate availability, size of dispersing unit), individual (age, body mass, pregnancy status), and environmental (rainfall) factors influence the three stages of dispersal in female meerkats. For this purpose, we monitored 65 dispersing units throughout the entire dispersal process. Specifically, we expected (1) a positive relationship between population density and daily emigration rates, (2) a negative effect of density on dispersal distance and time to settlement, and (3) association with unrelated males, dispersing unit size, and pregnancy status of dispersers to interact with density.

## METHODS

Our study was conducted between September 2013 and March 2017 at the Kalahari Meerkat Project (KMP) located on the Kuruman River Reserve (26°590 S, 21°500 E), South Africa. The region is characterized by low seasonal rainfalls between October and April and large daily and seasonal temperature variations (Clutton-Brock et al. 1998b). Temperature and precipitation data were available from on-site weather stations.

### *GPS data collection*

We fitted lightweight GPS radio-collars (<25 g, ~3.5% of meerkat body mass) to subordinate females a few days prior to, or immediately after, eviction from the natal group. The collars were composed of a VHF module (Holohil Systems, Carp, Ontario, Canada) and a GPS module (CDD, Athens, Greece). To mount the collars, individuals were sedated using a mixture of isoflurane and oxygen in compliance with the KMP protocol (Jordan et al. 2007). All necessary permits to handle and tag meerkats were granted to the KMP by the Department of Environment and Nature Conservation of South Africa and the Animal Ethics Committee of the University of Pretoria (permit "FAUNA 192/2014"). We used GPS locations to identify time of emigration and time of settlement, and to calculate dispersal distance and elapsed time between emigration and settlement. We distinguished emigration and settlement based on

visual investigation of the inflection points of the net squared displacement (NSD) plots (Cozzi et al. 2016). The NSD measures the square of the Euclidean distance from the place of eviction to any given GPS location along the dispersal path (Borger and Fryxell 2012). We further used field observations to validate the times of emigration and settlement identified by the NSD approach (see Appendix S1 for more details).

*Field data collection*

We located dispersing units by means of VHF radiotracking every two to seven days. At each visit, we recorded data on dispersing unit size, number of associated unrelated males, pregnancy status, and body mass. Study animals were part of a long-term research project, habituated to the presence of people, and trained to climb onto a portable weighing scale (Clutton-Brock et al. 1998b). Over the study period, we monitored a total of 65 female dispersing units. Dispersing units, i.e., any single female or group of related females evicted from the natal group, ranged from 1 to 6 females. Dispersing individuals were between 9 months and 5 yr of age at the time of eviction.

*Population density calculations*

Virtually all resident meerkat groups within the study area were known and censused during the study period. To estimate population density (individuals/km$^2$), we divided the number of all known resident individuals (i.e., total population size) by the size of the study area. Resident groups were visited by volunteers several times each week as part of the long-term activities at the KMP. At each visit, volunteers collected information on group composition and recorded GPS locations with handheld GPS devices (Garmin, Olathe, Kansas, United States). We defined the size of the study area as the combination of 95% kernel home ranges of all resident groups (Calenge 2006). A detailed description of the methods and smoothing parameter estimators can be found in Cozzi et al. (2018). All parameter calculations and statistical analyses were done in R (R Core Team 2013).

*Statistical modelling*

All analyses described here (1–4) were carried out at the dispersing unit level. We quantified the effects of social, individual, and environmental factors on (1) daily emigration probability, (2) daily return probability, and (4) daily settlement probability using three separate Cox proportional hazard models with mixed effects implemented in the function *coxme* of the R library *coxme* (Therneau 2018). The hazard rate $h[t]$, which in our case indicates the likelihood of transitioning from one stage to the next (e.g., transience to settlement) for a given time step, was calculated at daily intervals. We used time-dependent covariates where each day $t$ appears as a separate observation. To investigate (3) transience, we quantified the effects of the same factors on dispersal distance and dispersal time with two separate linear models using the function *lm* in R. In all four analyses (Cox proportional hazard and linear models), we used model selection to test all combinations of predictor variables. Model selection was based on Akaike's Information Criterion (AIC) and performed using the library *MuMin* (Barton 2018). Details for full models, outcomes of model selections, and descriptions of how we accounted for collinearity and temporal autocorrelation are given in the Appendices S2–S6.

*Emigration*

To investigate the daily emigration probability of dispersing units we only used units that emigrated from the natal territory. Units that died or were lost from the study before emigration were right censored (Fox and Weisberg 2011). We included *mass* and *age* of the oldest dispersing unit member, population density (*pop*) and its squared value ($pop^2$) to account for nonlinearity, rainfall (*rain*), the number of females in a dispersing unit (*female*), whether or not males were present (*male*), pregnancy status of unit members (*preg*), as well as the pregnancy status of the dominant female at the natal group (*pregnatal*), and biological meaningful interactions. We used the random terms *year*, the year in which a unit dispersed, and *origin*,

the natal group identity from which a unit originated. Further details on model parameters can be found in the Appendix S2.

*Return*

To investigate the daily return probability of dispersing units, we only used dispersing units that returned to their natal group (Appendix S3). Units that died or were lost were right-censored. We included the same explanatory variables used in the *Emigration* model: *mass*, *age*, *pop*, $pop^2$, *rain*, *female*, *male*, *preg*, and *pregnatal*. We fitted the random terms *year* and *origin*.

*Transience*

*Distance*. – We investigated the Euclidean dispersal distance between the emigration location and the location at settlement (Appendix S4). For this model and the *Time* model described in the next subsection, we only considered dispersing units that emigrated from their natal territory and settled in a new territory. We square-root transformed the response variable *dist* to meet assumptions of normality. We included *mass* and *age* at the time of emigration, and *pop*, $pop^2$, and *rain* at the time of settlement. We further included the association with males at the time of emigration (*male*) and the dispersing unit size (*unit*) at the time of settlement. Here, sample size was small because we included only dispersing units that emigrated, and we did not include random effects to avoid overfitting of the model. However, we tested for repeatability of measures across years (Stoffel et al. 2017) and did not detect repeatability.

*Time*. – We investigated the number of days elapsed between emigration and settlement (Appendix S5). The response variable *time* followed a square-root-normal distribution and was therefore square-root-transformed. We fitted the same explanatory variables used in the model *Distance*: *mass*, *age*, *pop*, $pop^2$, *rain*, *unit*, *male*. We performed this model on the same data set as the *Distance* model and did not include random effects (see explanation above).

*Settlement*

To investigate the settlement probability of dispersing units we only used dispersing units that emigrated from their natal territory (Appendix S6). Units that died or were lost were right-censored. The difference between this model and the models *Emigration* and *Return* is that time *t* represents the number of elapsed days since emigration and not since eviction. We included the following explanatory variables: *mass*, *age*, *pop*, $pop^2$, *rain*, *female*, *male*, and *preg*. We used the random terms *year* and *origin*.

**RESULTS**

Females were evicted from their natal groups either alone or as several females at a time, forming same-sex dispersing units that varied in size from one to six related females. Thirty-four of the 65 evicted dispersing units (52%) returned to their natal groups, after an average post-eviction phase of 26.4 d (interquartile range: 9–35 d). Twenty-six units (40%) emigrated from their natal territory, after an average post-eviction phase of 26.0 d (9–37 d). Three units died and two units were lost after eviction. Of the 26 units that emigrated, 18 units settled in a new territory after an average transience of 38.8 d (13–59 d), one died, three were lost, one joined another unit, and three returned to their natal group.

Due to very low rainfall during the wet season between October 2015 and April 2016, the population size dropped below 50% of the size observed at the start of the study, in September 2013. This produced a gradient in population density that varied between 1.7 and 4.2 individuals per $km^2$ during the 3.5-yr study period and offered an opportunity to study the effects of population density on each stage of female meerkat dispersal in a relatively short time frame. In Fig. 2A, we divided densities in three equal bins with similar sample size: low (1.7–2.8 individuals/$km^2$, n = 168), medium (2.8–3.5 individuals/$km^2$, n = 239), and high (3.5–4.2 individuals/$km^2$, n = 220) population densities.

*Emigration*

Daily rates of emigration varied with population density. We observed a nonlinear relationship between population density and emigration (Exponential coefficient β = 30.56, Estimate = 3.42, SE = 2.12, Appendix S2). Daily emigration probability was highest at low population density, lowest at medium densities and high again at high densities (Fig. 2A). After eviction, large dispersing units emigrated earlier from the natal territory than small units (Fig. 2A), and this effect was most pronounced at medium densities (β = 0.41, Est = 0.89, SE = 0.36). The presence of unrelated males increased the daily emigration probability of female dispersing units (β = 3.45, Est = 1.24, SE = 0.62), and this effect was stronger in large female units (β = 7.06, Est = 1.95, SE = 0.77, Fig. 2B). Amount of rain during the previous nine months decreased the daily probability of emigration (β = 0.65, Est = 0.43, SE = 0.22). Body mass of the oldest unit member, age of oldest unit member, and pregnancy status of the dominant female at the natal group did not influence daily emigration probability.

*Return*

Population density increased the daily probability that evicted units returned to their natal groups (β = 2.27, Est = 0.82, SE = 0.30). Such probability decreased with increasing age of the oldest unit member (β = 0.44, Est = 0.82, SE = 0.26), and when one or more females in the unit were pregnant (β = 0.51, Est = 0.68, SE = 0.45, Fig. 3A). When the dominant female in the dispersing unit's respective natal group was pregnant, return time to the natal group increased (β = 0.28, Est = 1.26, SE = 0.42). Return to the natal group was associated with increased rates of abortion in pregnant dispersing females. Sixty-two percent of pregnant dispersers aborted their litters before being accepted back in the natal group. Of the 38% of the successfully born litters, only 42% survived to the first month (Appendix S7). Rain during the previous nine months decreased the daily probability to return (β = 0.45, Est = 0.81, SE = 0.27). Body mass of the oldest unit member, unit size, and presence of males did not influence daily return probability of dispersing units.

*Transience*

*Distance*. – The average straight-line dispersal distance between emigration and settlement was 2.24 km (interquartile range: 1.08–2.66 km), and it was negatively correlated with dispersing unit size (Est = 7.45, SE = 1.63, Fig. 4A). Females that had grouped with males during the post-eviction phase settled closer to the natal territory than females that had not found males during this period (Est = 19.65, SE = 5.52, Fig. 4A). Rain in the nine months prior to settlement had a small negative effect on dispersal distance (Est = 0.14, SE = 0.05). Population density and body mass and age of the oldest unit members did not influence dispersal distance.

*Time*. – Dispersing units spent an average of 46 d (interquartile range 16–57 d) in transience before they settled. Population density was the only factor that influenced time to settlement. When population density was high, dispersing units spent more time until they settled (Est = 2.11, SE = 1.15, Fig. 4B). Rainfall, body mass, and age did not influence dispersal time.

*Settlement*

Daily rates of settlement varied with population density. During settlement, population density and rainfall were correlated; we therefore fitted two models to account for both variables separately: one including population density, but not rainfall (Appendix S6, Table S1a); and one including rainfall, but not population density (Appendix S6: Table S1b). The relationship between population density and daily settlement was not linear (β = 34,708.01, Est = 10.45, SE = 7.81, Appendix S6: Table S1a). Daily settlement probability was high at low population densities, low at medium densities, and high again at high densities (Appendix S6: Table S1a). Large dispersing units settled earlier than small units (β = 9.14, Est = 2.21, SE = 0.70, Appendix S6: Table S1a). The presence of unrelated males increased overall daily settlement probability (β = 27.18, Est = 3.30, SE = 1.86, Appendix S6: Table S1b), but this

effect was weaker the more females were present in a dispersing unit (β = 0.15, Est = 1.87, SE = 1.80). Pregnancies increased the daily settlement probability of dispersing units (β = 2,106.94, Est = 7.65, SE = 3.81, Fig. 3B). As opposed to females that returned to the natal group, females in dispersing units that emigrated successfully carried through 89% of their pregnancies, of which they only lost 35% within the first month (Appendix S7). Rain during the previous nine months decreased the daily probability of settlement (β = 0.33, Est = 1.10, SE = 0.59). Body mass and age of the oldest unit members did not affect daily settlement probability.

## DISCUSSION

Our study showed that interactions between social, individual, and environmental factors affected each of the three dispersal stages differently. Further, our findings emphasize the central role of population density on dispersal. We found that daily emigration probabilities were high at low and high population densities, and lowest at medium densities, suggesting a nonlinear relationship. Increasing population density also resulted in increased time spent in the transient stage. The size of the dispersing unit had a positive effect on daily emigration and settlement probabilities, and large units emigrated earlier than small units. We further showed that dispersal distance decreased with increasing numbers of females present in a dispersing unit and when unrelated males were present. These social factors were more important drivers of dispersal than individual characteristics such as body mass and age of the oldest unit member, with the latter only influencing daily return probabilities of dispersers.

Our findings are consistent with the theoretical predictions that the limited benefits of cooperation at low population density can enhance emigration rate in social species (Hoogland 2013), and that at moderate densities, where the benefits of cooperation are expected to increase and exceed the costs of kin competition, individuals are more likely to remain in the natal patch (Clutton-Brock 2002, Matthysen 2005). Finally, the increased emigration rate at high densities may be best explained by increasing costs of kin competition that exceed the benefits of

cooperation (Cote et al. 2007). A similar nonlinear relationship has been proposed in other systems (Kim et al. 2009, Rousset 2012). The negative relationship between population density and emigration at low population size suggests that meerkats are subject to an Allee effect, i.e., inverse density dependence at low density (Allee et al. 1949), which can be caused by different factors such as inbreeding, demographic stochasticity, or a reduction of cooperative interactions when fewer individuals are present (Courchamp et al. 1999). In the cooperatively breeding meerkat, inverse density dependence potentially decreased inclusive fitness and promoted emigration to escape the consequences of an Allee effect induced by reduced cooperation.

Our results showing negative density-dependent emigration, transience time, and settlement support the theoretical prediction that population density promotes the evolution of delayed dispersal and philopatry in cooperative breeders (Kokko and Lundberg 2001, Platt and Bever 2009). In many species, aggression from conspecifics is predicted to increase, and chances of finding vacant territory to decrease with increasing density (Lambin et al. 2001). Thus, staying at home and gaining inclusive fitness through cooperation can be an adaptive life-history strategy when vacancies are unavailable (Kokko and Lundberg 2001). In meerkats, this hypothesis is further supported by the fact that evicted females were more likely to return to the natal group at high population densities, and by previous findings, showing that dispersing meerkats avoided areas where conspecifics were found (Cozzi et al. 2018). We found higher emigration and settlement rates after periods with low rainfall. Our results therefore do not support the hypothesis that diminished body condition due to low rainfall promotes the evolution of delayed dispersal (Jarvis et al. 1994, Molteno and Bennett 2006). We suggest that the local depletion of resources caused by low rainfall increases competition over limited resources and forces individuals to leave their natal site (Greenwood 1980).

We observed an important effect of mate availability during different stages of the dispersal event. Those females that associated with unrelated males in the early stages of the

dispersal event (i.e., post-eviction) were characterized by early emigration rate and reduced dispersal distance, while those who did not associate with unrelated males either delayed emigration or dispersed a considerable distance. Most of the males that joined females during post-eviction were from outside the study area (N. Maag, *personal observ*ation), suggesting that males travelled longer distances than females, who generally settled close to the natal territory (Fig. 4A). Male-biased dispersal and female philopatry is widespread in mammals and suggested to avoid inbreeding (Pusey 1987, Long et al. 2008). Females dispersed further if they did not associate with males during post-eviction, possibly to reduce the risk of inbreeding if no unrelated males were available at the onset of dispersal. Mate availability seems to be more important for the dispersal decision of meerkats than individual traits such as body mass, although the latter was shown to be important within and across other species (Jenkins et al. 2007, Delgado et al. 2010, Debeffe et al. 2012, Stevens et al. 2014). Our findings are in line with a recent study showing that, in a social species, the distribution of breeding partners was more important for dispersal patterns than individual phenotypes (Davidian et al. 2016). However, to assess the influence of phenotypic traits on dispersal, an investigation at the individual level may be more informative.

Dispersing in large coalitions may reduce the costs of traveling away from the natal group and increase the competitive abilities of dispersers during transience and settlement (Bernasconi and Strassmann 1999, Boswell et al. 2001). After settlement, having several helpers present will likely increase reproductive success and improve group augmentation (Clutton-Brock et al. 1999, Kokko et al. 2001, Russell et al. 2002). Our results, showing that large dispersing coalitions had higher daily emigration and settlement probabilities than small coalitions and single females, are consistent with the assumption that increased coalition size is beneficial for dispersal in social species. Large coalitions emigrated earlier than small coalitions when population density was most restrictive (i.e., at medium densities, Fig. 2A), suggesting a competitive advantage with increasing coalition size. This is because aggression

from conspecific residents increases at higher densities and larger coalitions are more likely to win aggressive encounters (Packer et al. 1990, Wilson et al. 2002, Young 2004). In addition, traveling with other individuals can reduce the costs (i.e., body mass, stress hormones, immune defence, survival) induced during extra-territorial forays or floating that often precede dispersal (Creel and Creel 2002, Young 2004, Ridley et al. 2008). Due to the difficulty of following dispersers, however, the effect of coalition size on body condition during the later stages of dispersal was never quantified and remains to be tested empirically.

In most cooperative species, a single dominant female monopolizes group reproduction (Koenig and Dickinson 2004, Clutton-Brock et al. 2010). However, subordinates occasionally breed thereby reducing the fitness of the dominant individual (Koenig and Dickinson 2004). Dominant individuals may therefore attack subordinates to induce chronic stress and reduce their fertility (Wingfield et al. 1991, Creel 2001). However, several studies have shown that dominant individuals had higher stress hormone levels than subordinates and suggested that reproductive suppression is not maintained through social stress (Abbott et al. 1997, Creel 2001). In meerkats, temporary evictions of subordinate females were previously shown to increase their stress levels and abortion rates (Young et al. 2006). Our results confirm Young et al. (2006) findings and provide further support for the stress-related suppression hypothesis. In addition, we provide new insight into the outcome of pregnancies when subordinates emigrate instead of return. The daily probability of settlement increased substantially if an emigrant female was pregnant (Fig. 3B), and emigrants mostly remained pregnant during transience and successfully gave birth after settlement (Appendix S7). Pregnant females may be forced to promptly find vacant territories for settlement in a shorter period so parturition can occur in a permanent burrow, as a safe territory is crucial for offspring growth and survival (Bronson 1985, Clutton-Brock et al. 1989). Survival of the first litter may be crucial for fast group augmentation and successful group establishment, as offspring from the first litter will increase success of the following litters (Clutton-Brock et al. 2001).

In conclusion, we propose that both cooperation (at low numbers) and kin competition (at high numbers) are responsible for the nonlinear effect of population density on daily emigration and settlement rates of female meerkats (Platt and Bever 2009, Hoogland 2013). A nonlinear relationship between population density and dispersal can also occur in non-social species, although it may be caused by different factors such as low mate availability and resource competition (Loe et al. 2009, Rousset 2012). During transience and settlement, a negative association between population density and dispersal may be expected for various vertebrate species (Lambin et al. 2001, Wilson et al. 2017). Different species may, however, show different reactions to population density. For example, non-territorial species, such as marine birds, show a positive relationship between population density and settlement probability, because patches with high density correspond to areas of high resource abundance (Fernandez-Chacon et al. 2013). Although we suggest that the negative association between meerkat dispersal and population density is due to a reduction in cooperation at home and increased chances of finding vacant territory (Kokko and Lundberg 2001, Platt and Bever 2009), alternative factors such as the spatial distribution of resources may play an important role (McPeek and Holt 1992, Baguette et al. 2011). Where resources are not uniformly distributed, for example when resources become abundant in a previously unoccupied, but now suitable habitat (e.g., invasion during range expansion), emigration rate may increase at lower densities (Travis et al. 2009). Future studies investigating the effect of social, individual, and environmental factors on all three stages of dispersal will improve our understanding of the effect of population density and other drivers on dispersal and consequently population dynamics.

## ACKNOWLEDGEMENTS

Funding for this study was provided by the Swiss National Science Foundation (Project CR32I3_159743). We thank the Northern Cape Conservation Authority for permission to conduct this research, and the farmers neighbouring the Kuruman River Reserve for granting

us access to their private land. We thank the field managers and volunteers for facilitating field work and helping with data collection, in particular David Gaynor and Tim Vink. Special thanks go to our field assistants David Seager, Ana Morales Gonzalez, Hector Ruiz Villar, Peter Clark, Luc Le Grand, and Louis Bliard. We thank Marta Manser and Luca Borger for numerous discussions and comments on the manuscript, and Jeffrey Hostetler for help with statistical analysis. Our research relied on records of individual identities and life histories of meerkats, and research facilities maintained by the Kalahari Meerkat Project, which has been supported by the European Research Council (Research Grant No 294494 to T. H. Clutton-Brock), the University of Zurich and the Mammal Research Institute at the University of Pretoria.

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**FIGURES**

*Figure 1*. Schematic representation of female meerkat dispersal. During pregnancy, a dominant female typically evicts one or several subordinate females from the natal group. Evicted females remain in the natal territory (large grey circle) for a variable period (post-eviction phase). At the end of the post-eviction phase, females return to the natal group or emigrate from the natal territory. Returners help to raise the offspring of the dominant female and emigrants enter transience, settle in new territory (small grey circle), and breed.

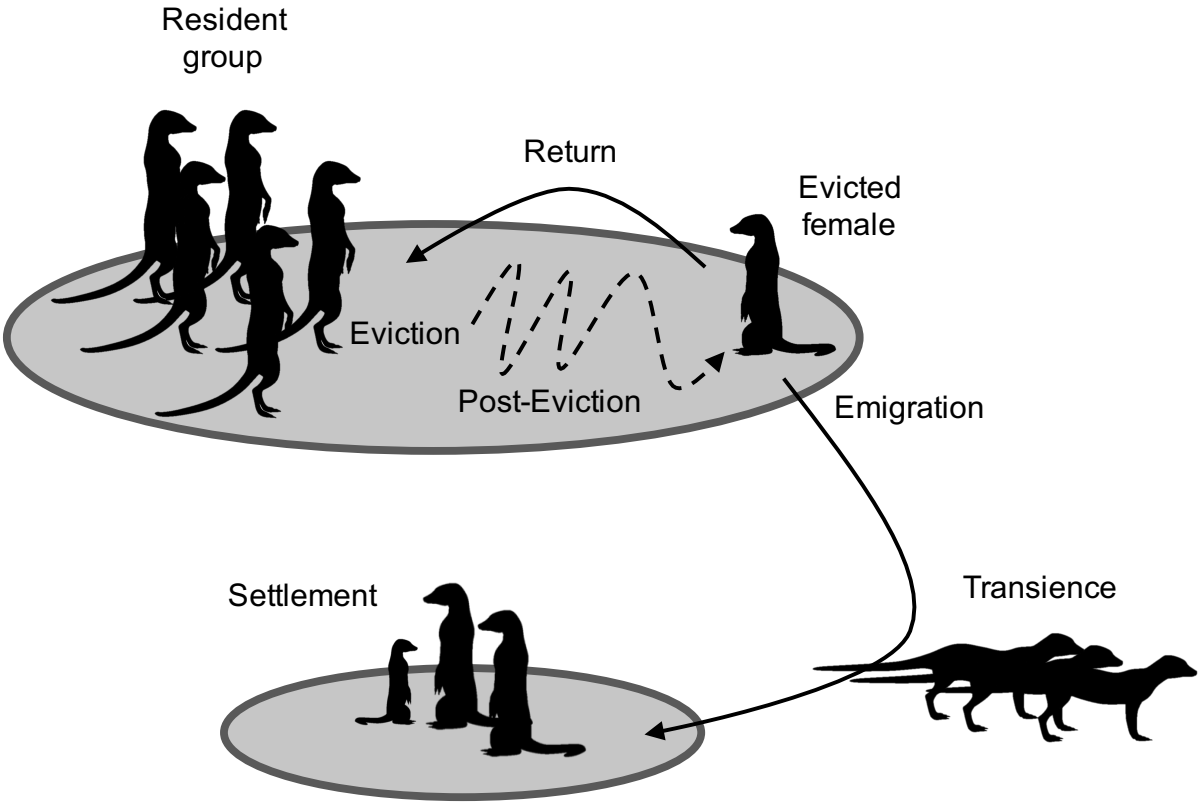


*Figure 2*. (A) Kaplan-Meier plot showing the effect of number of female meerkats (single evicted female, 1; two or more females grouped together in a coalition, 2+) on daily emigration probability at low (red), medium (light blue), and high population densities (dark blue). (B) Kaplan-Meier plot showing the effect of number of female meerkats on daily emigration rate in the absence (green) or presence of unrelated males (purple).

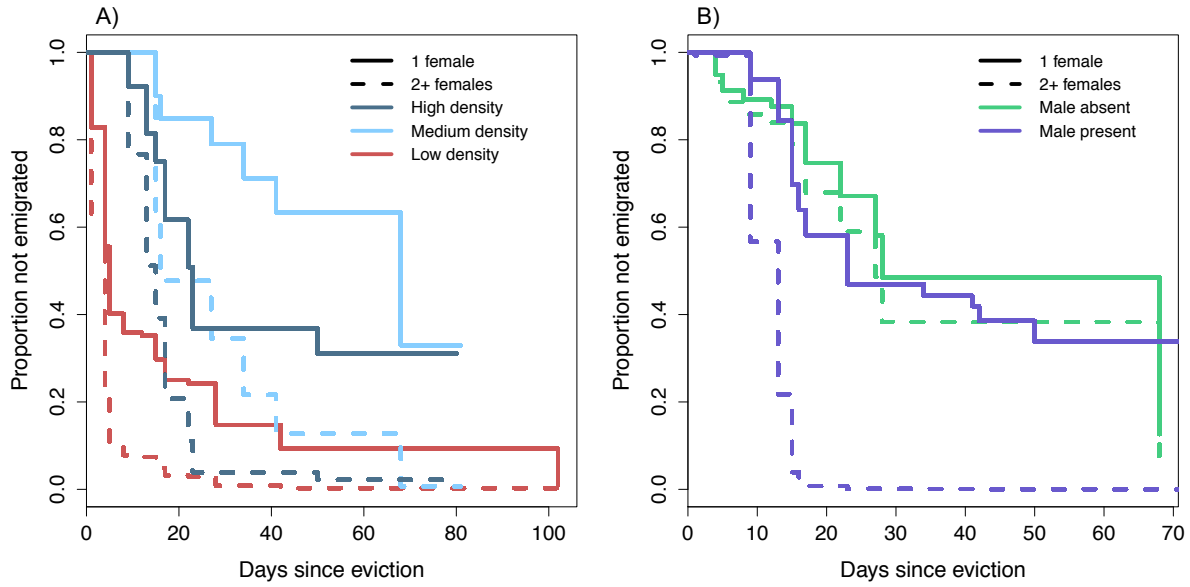


*Figure 3*. (A) Kaplan-Meier plot showing the effect of pregnancy (at least one female in the dispersing coalition is pregnant) on daily return probability of evicted female meerkats, including only those that returned to their natal group (34 out 65 coalitions). (B) Kaplan-Meier plot showing the effect of meerkat pregnancies on daily settlement probability.

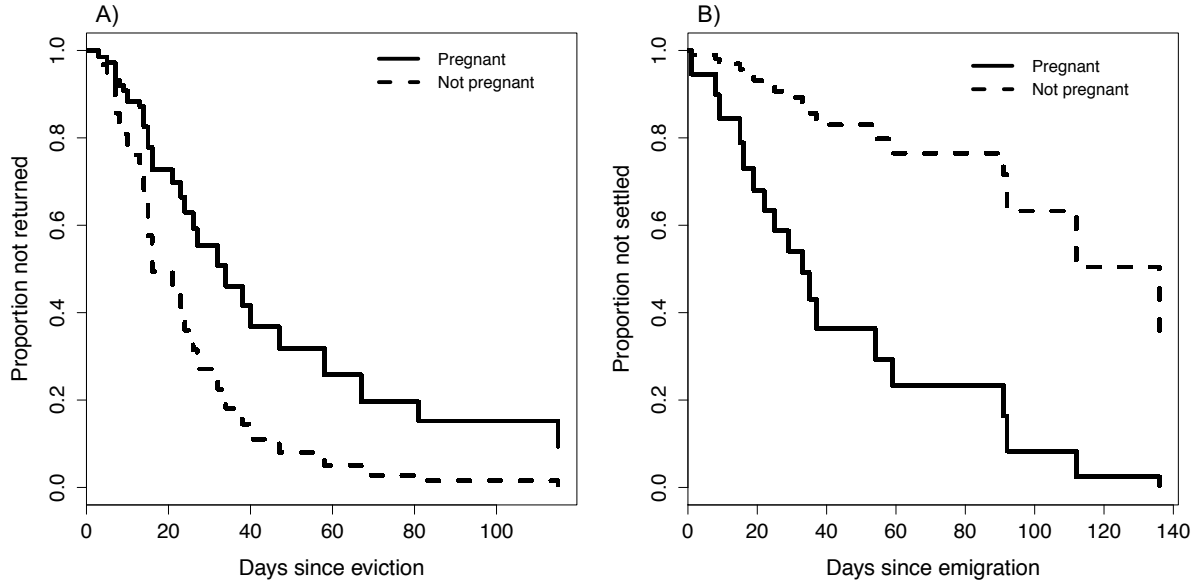
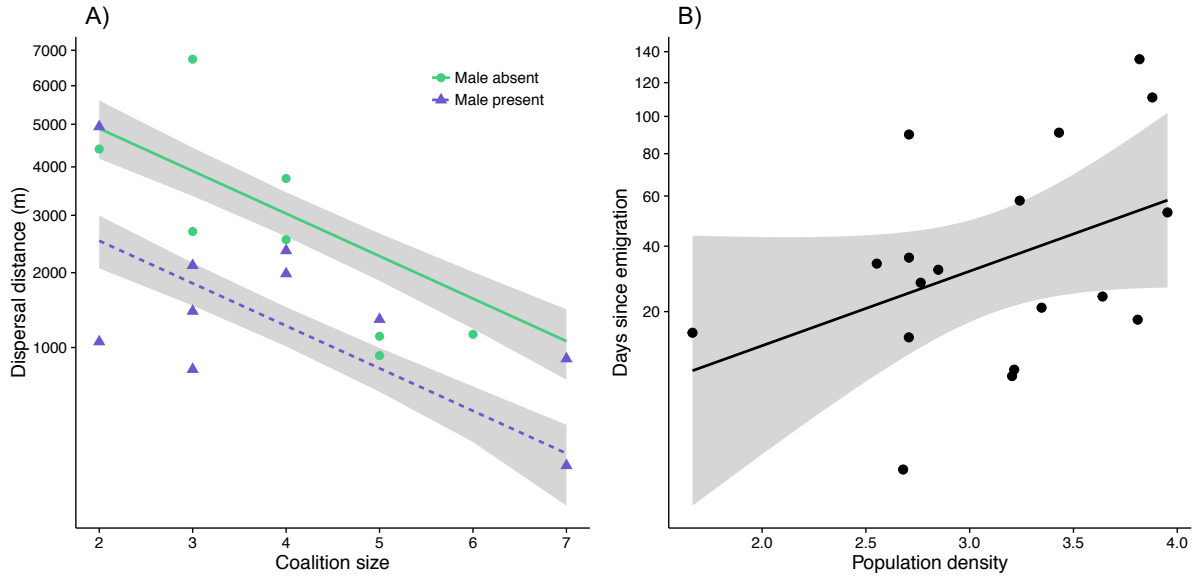


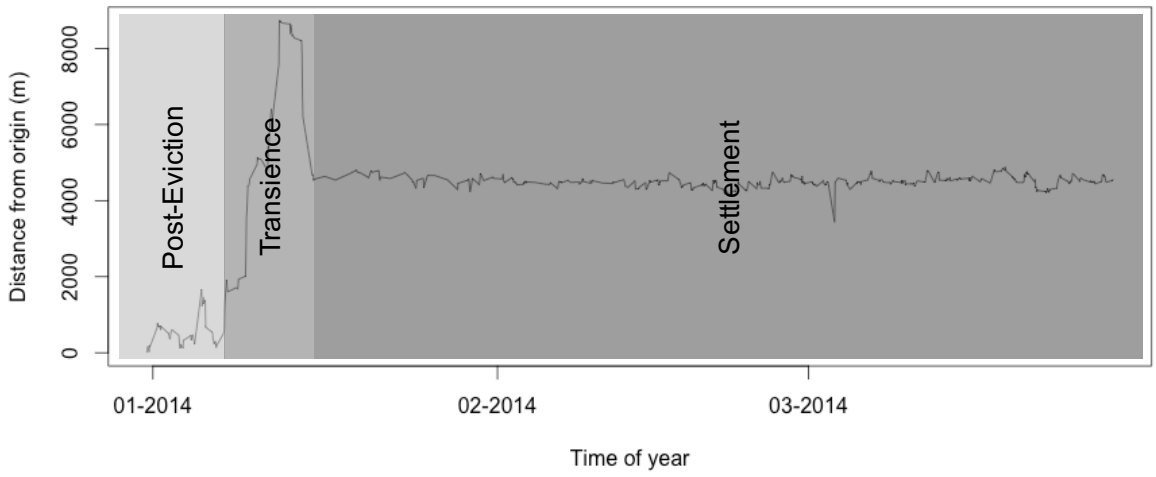
*Figure 4*. (A) Effect of mean meerkat coalition size (females and unrelated males) on net displacement (square-root transformed) between place of eviction and place of settlement. Female meerkats that did not group with males during post-eviction are shown in green, females that grouped with males during post-eviction are shown in purple. (B) Effect of population density (individuals per $km^2$) on female meerkats' dispersal time between emigration and settlement (in days, log transformed). Lines show predicted values and grey shaded areas show 95% confidence intervals.



## SUPPORTING INFORMATION

**Appendix S1:** Net displacement curve of dispersing meerkats

*Figure S1*. Characteristic dispersal curve of dispersing female meerkats quantified by net displacement (distance to natal site). The post-eviction phase starts after the eviction event and is characterized by typical territorial movement patterns, where female meerkats remain in the natal territory and distances covered per day resemble those of the natal group. Emigration marks the beginning of transience, where individuals cover farther distances per day and move away from the natal site. The time of settlement can clearly be identified by a change to territorial movement patterns.




Variations in NSD over time can be used to characterize transitions from one dispersal stage to the next. For each dispersing unit (lone female or multiple-member coalition), we calculated the NSD as the square of the Euclidean distance from the place of eviction to any given GPS location along the entire dispersal path. We then visually investigated the resulting NSD plots for inflection points (Cozzi et al. 2016)[1], which corresponded to time of emigration and time

[1] Cozzi, G., M. Chynoweth, J. Kusak, E. Çoban, A. Çoban, A. Ozgul, and Ç. H. Şekercioğlu. 2016. Anthropogenic food resources foster the coexistence of distinct life history strategies: year-round sedentary and migratory brown bears. Journal of Zoology 300:142–150.

of settlement. We used field observations to validate results from the NSD approach. Successful emigration was typically characterized by unidirectional exploratory movements and lack of attempts to reunite with the natal group. Successful settlement coincided with the use of the same sleeping burrow for extended periods (>1 week) accompanied by normal foraging behaviour resembling territorial behaviour.

**Appendix S2:** Cox proportional mixed effects model *Emigration*

*Table S1*. Upper table: description of the full statistical model and model variables of the Cox proportional mixed effects model *Emigration*. Middle table: results from model selection based on Akaike's information criterion (models from subset = delta<3 are shown); DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model based on AICc; W = Akaike weights. Lower table: details of best model; Coef = coefficient; β = exponential coefficient; SE = standard error of Coef; Z = ratio of regression coefficient to standard error; Importance = relative importance of each variable; Chi = Chi-square score.

| Response | Explanatory | Variable description | Random |
|---|---|---|---|
| *Surv(start, stop, emi)* | *pop* | Population density (individuals per km$^2$) | *year* |
| | *pop$^2$* | Nonlinear effect of population density | *origin* |
| | *mass* | Body mass of the oldest unit member, because the oldest female often assumes dominancy and makes movement decisions (N. Maag, *pers. obs.*) | |
| | *age* | Age of the oldest coalition member | |
| | *rain* | Rain sum of the previous 9 months (after testing for rain effects at one and three months, see English et al. 2012) | |
| | *female* | Number of females in dispersing together | |
| | *male* | Factor: male present, absent | |
| | *preg* | Factor: 1 = at least one female pregnant, 0 = none pregnant | |
| | *pregnatal* | Factor: 1 = dominant fem. at natal group pregnant, 0 = not pregnant | |
| | *female:pop$^2$* | | |
| | *female:male* | | |

| Variable | DF | AICc | ΔAICc | W |
|---|---|---|---|---|
| *male+pop$^2$+pop+rain+female+female:male+female:pop$^2$* | 7 | 104.57 | 0.00 | 0.42 |
| *male+preg+pop$^2$+pop+rain+female+female:male+female:pop$^2$* | 8 | 104.71 | 0.14 | 0.39 |
| *male+pop$^2$+pop+female+female:male+female:pop$^2$* | 13 | 106.11 | 1.53 | 0.19 |

| Variable | Coef | β | SE | Z | Importance | |
|---|---|---|---|---|---|---|
| *pop* | -3.99 | 0.02 | 2.08 | -1.92 | 1.00 | Chi = 30.42 |
| *pop²* | 3.42 | 30.56 | 2.12 | 1.61 | 1.00 | |
| *female* | -0.50 | 0.60 | 0.45 | -1.12 | 1.00 | |
| *male(present)* | 1.24 | 3.45 | 0.62 | 1.99 | 1.00 | |
| *female:male(present)* | 1.95 | 7.06 | 0.77 | 2.55 | 1.00 | |
| *female:pop²* | -0.89 | 0.41 | 0.36 | -2.49 | 1.00 | |
| *rain* | -0.43 | 0.65 | 0.22 | -1.96 | 0.81 | |

The Cox regression assumes that the probability per unit of time that a dispersing unit emigrates, returns, or settles (hazard rate = $h[t]$), is the product of a baseline probability and a factor representing the joint effect of the covariates, with $t$ representing the number of days since the females were evicted. The β values reported in the Cox models *Emigration*, *Return*, and *Settlement* are called exponential coefficients and can be interpreted as the multiplicative effect of each explanatory variable on the hazard (Fox and Weisberg 2011)[2].

Continuous variables were standardised by subtracting their mean and then dividing by their standard deviation in all three Cox models (Appendices S2, S3, S6). To ensure that predictor variables were not correlated with each other, we calculated variance inflation factors (Belsley et al. 2004)[3] for all predictor coefficients in the full models. For each dispersing unit, we obtained autocorrelation functions (Pinheiro and Bates 2000)[4] from model residuals to test for temporal autocorrelation. Model residuals were not correlated across time in any of the dispersing units.

*Age* and *mass* were not available for all individuals. We therefore performed initial model selection on a reduced dataset, including only dispersing units for which *age* and *mass* of the oldest unit member were available. If one or both variables dropped out during initial model

[2] Fox, J., and S. Weisberg. 2011. An R Companion to Applied Regression. SAGE Publications, Thousand Oaks, California, USA.
[3] Belsley, D. A., Kuh, E., and R. E. Welsch. 2005. Regression Diagnostics: Identifying Influential Data and Sources of Collinearity. John Wiley & Sons, Hoboken, New Jersey, USA.
[4] Pinheiro, J., and D. Bates. 2000. Mixed-effects models in S and S-PLUS. First edition. Springer-Verlag, New York, New York, USA.

selection and were therefore shown to have no influence on the response variable, we repeated the model selection with the full dataset. This is to avoid losing too many observations and unnecessarily reducing sample size. In cases where *age* and *mass* had an effect (did not drop out during initial model selection), we continued with the reduced subset of the data. We used the same approach in all models (Appendices S2-S6), and the sample sizes for the number of dispersing units in which the *age* and *mass* were known are given here:

| Model | Appendix | Total # units | Age available # units | Mass available # units |
|---|---|---|---|---|
| *Emigration* | S2 | 31 | 30 | 23 |
| *Return* | S3 | 39 | 35 | 27 |
| *Distance* | S4 | 18 | 18 | 13 |
| *Time* | S5 | 18 | 18 | 13 |
| *Settlement* | S6 | 22 | 22 | 15 |

**Appendix S3:** Cox proportional mixed effects model *Return*

*Table S1*. Upper table: description of the full statistical model and model variables of the Cox proportional mixed effects model *Return*. Middle table: results from model selection based on Akaike's information criterion (models from subset = delta<3 are shown); DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model based on AICc; W = Akaike weights. Lower table: details of best model; Coef = coefficient; β = exponential coefficient; SE = standard error of Coef; Z = ratio of regression coefficient to standard error; Importance = relative importance of each variable; Chi = Chi-square score.

| Response | Explanatory | Variable description | Random |
|---|---|---|---|
| *Surv(start, stop, ret)* | *pop* | Population density (individuals per km$^2$) | *year* |
| | *pop$^2$* | Nonlinear effect of population density | *origin* |
| | *mass* | Body mass of the oldest unit member, because the oldest female often assumes dominancy and makes movement decisions (N. Maag, *pers. obs.*) | |
| | *age* | Age of the oldest coalition member | |
| | *rain* | Rain sum of the previous 9 months (after testing for rain effects at one and three months, see English et al. 2012) | |
| | *female* | Number of females in dispersing together | |
| | *male* | Factor: male present, absent | |
| | *preg* | Factor: 1 = at least one female pregnant, 0 = none pregnant | |
| | *pregnatal* | Factor: 1 = dominant fem. at natal group pregnant, 0 = not pregnant | |
| | *female:pop$^2$* | | |
| | *female:male* | | |

| Variable | DF | AICc | ΔAICc | W |
|---|---|---|---|---|
| *pregnatal+preg+pop+rain+age* | 5 | 148.86 | 0.00 | 0.25 |
| *pregnatal+pop+rain+age* | 4 | 149.20 | 0.34 | 0.21 |
| *pregnatal+male+preg+pop+rain+age* | 6 | 150.66 | 1.80 | 0.10 |
| *pregnatal+preg+pop+rain+age+female* | 6 | 150.88 | 2.02 | 0.09 |
| *pregnatal+preg+pop$^2$+pop+rain+age* | 6 | 150.88 | 2.03 | 0.09 |
| *pregnatal+pop+rain+age+female* | 5 | 151.08 | 2.23 | 0.08 |
| *pregnatal+male+pop+rain+age* | 5 | 151.13 | 2.27 | 0.08 |
| *pregnatal+pop$^2$+pop+rain+age* | 5 | 151.15 | 2.30 | 0.08 |

| Variable | Coef | β | SE | Z | Importance | |
|---|---|---|---|---|---|---|
| *pop* | 0.82 | 2.27 | 0.30 | 2.76 | 1.00 | Chi = 21.73 |
| *rain* | -0.81 | 0.45 | 0.27 | -3.02 | 1.00 | |
| *age* | -0.82 | 0.44 | 0.26 | -3.08 | 1.00 | |
| *pregnatal(1)* | -1.26 | 0.28 | 0.42 | -2.99 | 1.00 | |
| *preg(1)* | -0.68 | 0.51 | 0.45 | -1.51 | 0.54 | |

Because *age* was not dropped during model selection, this analysis was performed with a reduced dataset that excluded dispersing units for which age was unavailable (see explanation above, Appendix S2).

**Appendix S4:** Linear model *Distance*

*Table S1.* Upper table: description of the full statistical model and model variables of the linear model *Distance*. Middle table: results from model selection based on Akaike's information criterion (models from subset = delta<4 are shown); DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model based on AICc; W = Akaike weights. Lower table: details of best model; SE = standard error of model estimate; Importance = relative importance of each variable; $R^2$ = multiple R squared.

| *Response* | *Explanatory* | Variable description |
|---|---|---|
| *sqrt(netdispl)* | *pop* | Population density (individuals per km$^2$) |
| | *pop$^2$* | Nonlinear effect of population density |
| | *mass* | Body mass of the oldest unit member, because the oldest female often assumes dominancy and makes movement decisions (N. Maag, *pers. obs.*) |
| | *age* | Age of oldest female in months |
| | *rain* | Rain sum of the previous 9 months (after testing for rain effects at one and three months, see English et al. 2012) |
| | *unit* | Size of dispersing unit (female + male) at time of settlement |
| | *male* | Factor: male present, absent at time of departure |

| Variable | DF | AICc | ΔAICc | W |
|---|---|---|---|---|
| *rain+unit+male* | 5 | 146.19 | 0.00 | 0.87 |
| *rain+age+unit+male* | 6 | 150.03 | 3.84 | 0.13 |

| Variable | Estimate | SE | Importance | |
|---|---|---|---|---|
| *intercept* | 102.73 | 11.01 | | $R^2 = 0.71$ |
| *unit* | -7.45 | 1.63 | 1.00 | |
| *male(present)* | -19.65 | 5.52 | 1.00 | |
| *rain* | -0.14 | 0.05 | 1.00 | |

In this model and the *Time* model described below (Appendix S5), we calculated correlation coefficients for each pair of predictor variables and tested for significance to ensure that predictor variables were not correlated with each other.

**Appendix S5:** Linear model *Time*

*Table S1.* Upper table: description of the full statistical model and model variables of the linear model *Time*. Middle table: results from model selection based on Akaike's information criterion (models from subset = delta<3 are shown); DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model based on AICc; W = Akaike weights. Lower table: details of best model; SE = standard error of model estimate; Importance = relative importance of each variable; $R^2$ = multiple R squared.

| *Response* | *Explanatory* | Variable description |
|---|---|---|
| *sqrt(time)* | *pop* | Population density (individuals per km$^2$) |
| | *pop$^2$* | Nonlinear effect of population density |
| | *mass* | Body mass of the oldest unit member, because the oldest female often assumes dominancy and makes movement decisions (N. Maag, *pers. obs.*) |
| | *age* | Age of oldest female in months |
| | *rain* | Rain sum of the previous 9 months (after testing for rain effects at one and three months, see English et al. 2012) |
| | *unit* | Size of dispersing unit (female + male) at time of settlement |
| | *male* | Factor: male present, absent at time of departure |

| Variable | DF | AICc | ΔAICc | W |
|---|---|---|---|---|
| *pop* | 3 | 94.08 | 0.00 | 0.34 |
| *Null* | 2 | 94.60 | 0.52 | 0.26 |
| *unit* | 3 | 96.10 | 2.02 | 0.12 |
| *pop+rain* | 4 | 96.52 | 2.44 | 0.10 |
| *pop$^2$+pop* | 4 | 96.73 | 2.65 | 0.09 |
| *rain* | 3 | 96.83 | 2.75 | 0.09 |

| Variable | Estimate | SE | Importance | |
|---|---|---|---|---|
| *intercept* | -0.71 | 3.65 | | $R^2$ = 0.17 |
| *pop* | 2.11 | 1.15 | 0.53 | |

**Appendix S6:** Cox proportional mixed effects model *Settlement*

Due to collinearity between population density and rainfall, we performed two models: in S1a we fitted population density, in S1b we fitted rainfall. Upper tables: description of the full statistical models and model variables of the Cox proportional mixed effects models *Settlement* S1a and S1b. Middle tables: results from model selection based on Akaike's information criterion (models from subset = delta<3 are shown); DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model based on AICc; W = Akaike weights. Lower tables: details of best model; Coef = coefficient; β = exponential coefficient; SE = standard error of Coef; Z = ratio of regression coefficient to standard error; Importance = relative importance of each variable; Chi = Chi-square score.

*Table S1a.* Cox proportional hazard model *Settlement* fitted with population density, but not with rainfall (due to correlation between *pop* and *rain*).

| Response | Explanatory | Variable description | Random |
|---|---|---|---|
| *Surv(start, stop, set)* | *pop* | Population density (individuals per km$^2$) | *year* |
| | *pop$^2$* | Nonlinear effect of population density | *origin* |
| | *mass* | Body mass of the oldest unit member, because the oldest female often assumes dominancy and makes movement decisions (N. Maag, *pers. obs.*) | |
| | *age* | Age of the oldest coalition member | |
| | *female* | Number of females in dispersing together | |
| | *male* | Factor: male present, absent | |
| | *preg* | Factor: 1 = at least one female pregnant, 0 = none pregnant | |
| | *female:pop$^2$* | | |
| | *female:male* | | |

| Variable | DF | AICc | ΔAICc | W |
|---|---|---|---|---|
| *preg+pop$^2$+pop+female* | 14 | 47.41 | 0.00 | 0.34 |
| *preg+pop$^2$+pop+age+female* | 15 | 48.23 | 0.82 | 0.22 |
| *preg+pop$^2$+pop+female+female:pop$^2$* | 15 | 48.52 | 1.11 | 0.19 |
| *preg+pop+age+female* | 14 | 49.12 | 1.71 | 0.14 |
| *preg+pop$^2$+pop+age+female+female:pop$^2$* | 16 | 49.74 | 2.33 | 0.10 |

| Variable | Coef | β | SE | Z | Importance | |
|---|---|---|---|---|---|---|
| *pop* | -11.35 | 0.00 | 8.62 | -1.32 | 1.00 | Chi = 15.24 |
| *female* | 2.21 | 9.14 | 0.70 | 3.17 | 1.00 | |
| *preg(1)* | 7.65 | 2106.94 | 4.36 | 1.76 | 1.00 | |
| *pop²* | 10.45 | 34708.01 | 7.81 | 1.34 | 0.86 | |

*Table S1b.* Cox proportional hazard model *Settlement* fitted with rainfall, but not with population density (due to correlation between *pop* and *rain*).

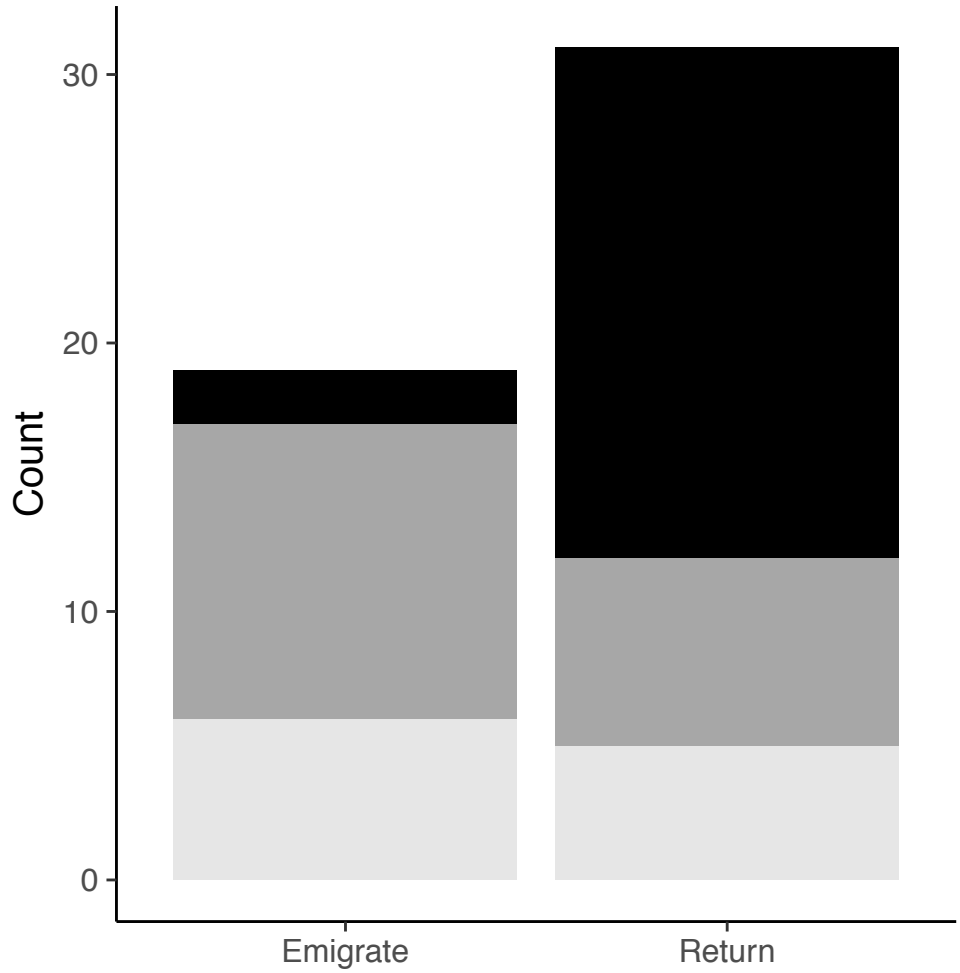
| Response | Explanatory | Variable description | Random |
|---|---|---|---|
| *Surv(start, stop, set)* | *mass* | Body mass of the oldest unit member, because the oldest female often assumes dominancy and makes movement decisions (N. Maag, *pers. obs.*) | *year* |
| | *age* | Age of the oldest coalition member | *origin* |
| | *rain* | Rain sum of the previous 9 months (after testing for rain effects at one and three months, see English et al. 2012) | |
| | *female* | Number of females in dispersing together | |
| | *male* | Factor: male present, absent | |
| | *preg* | Factor: 1 = at least one female pregnant, 0 = none pregnant | |
| | *female:male* | | |

| Variable | DF | AICc | ΔAICc | W |
|---|---|---|---|---|
| *male+preg+rain+female+female:male* | 13 | 48.02 | 0.00 | 0.38 |
| *preg+rain+age+female* | 12 | 48.60 | 0.58 | 0.29 |
| *male+preg+rain+age+female+female:male* | 14 | 49.04 | 1.03 | 0.23 |
| *male+preg+rain+female* | 12 | 50.62 | 2.60 | 0.10 |

| Variable | Coef | β | SE | Z | Importance | |
|---|---|---|---|---|---|---|
| *rain* | -1.10 | 0.33 | 0.59 | -1.86 | 1.00 | Chi = 23.95 |
| *female* | 3.53 | 34.03 | 1.96 | 1.80 | 1.00 | |
| *preg(1)* | 8.93 | 7572.18 | 2.86 | 3.13 | 1.00 | |
| *male(1)* | 3.30 | 27.18 | 1.86 | 1.77 | 0.71 | |
| *female:male(1)* | -1.87 | 0.15 | 1.80 | -1.04 | 0.61 | |

**Appendix S7:** Pregnancy outcomes

*Figure S1.* Meerkat pregnancy outcomes depending on whether evicted female emigrated (left bar) or returned to their group (right bar). Aborted litters are shown in black, litters that were born and survived until the first month are shown in dark grey, litters that were born but lost before one month are shown in light grey.



# CHAPTER THREE

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## Cost of dispersal in a social mammal – body mass loss and increased stress

*Proceedings of the Royal Society B (in review)*

Photo credit: Nino Maag

# Cost of dispersal in a social mammal – body mass loss and increased stress

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**ABSTRACT**

Dispersal is a key process influencing the dynamics of socially and spatially structured populations. Dispersal success is determined by the state of individuals at emigration and the costs incurred after emigration. However, quantification of such costs is often difficult, due to logistical constraints of following wide-ranging individuals. We investigated the effects of dispersal on individual body mass and stress hormone levels in a cooperative breeder, the meerkat (*Suricata suricatta*). We measured body mass and faecal glucocorticoid metabolite (fGCM) concentrations from 95 dispersing females in 65 coalitions through the entire dispersal process. Females that successfully settled lost body mass, while females that did not settle but returned to their natal group after a short period of time did not. Furthermore, dispersing females had higher fGCM levels than resident females, and this was especially pronounced during the later stages of dispersal. By adding information on the transient stage of dispersal and by comparing dispersers that successfully settled to dispersers that returned to their natal group, we expand on previous studies focusing on the earlier stages of dispersal. We propose that body mass and stress hormone levels are good indicators to investigate dispersal costs, as these traits often play an important role in mediating the effects of the environment on other life-history events and individual fitness.

**Keywords:** Dispersal stage, glucocorticoid metabolites, individual trait, life history, meerkat

## INTRODUCTION

Dispersal is an important life-history process typically consisting of three stages: emigration from a natal territory, transience through an unfamiliar landscape, and settlement in a new area [1,2]. At each stage, dispersing individuals incur costs resulting from different individual, social, and environmental factors, and these costs influence the outcome of dispersal and consequently the associated population dynamics [1,3]. Costs of dispersal have been typically measured in the form of changes in survival and reproductive rates [3–5]. However, the effects of social and environmental factors on survival and reproduction are often mediated by morphological and physiological traits [6–8]. As such, a more mechanistic understanding of dispersal costs can be achieved by investigating traits such as body mass and stress hormone levels, which are known to correlate with individual fitness [9,10].

A variety of processes can be expected to influence body mass and stress hormone levels during dispersal [3]. For instance, unfamiliarity with a new area may result in reduced feeding efficiency [11], which may lead to loss in body mass and increased stress hormone levels. Unfamiliar territory often comes with higher susceptibility to predators, which might be reflected in further elevated stress levels [12]. Furthermore, dispersers are often exposed to aggression from resident conspecifics [13,14], and attacks may lead to wounds and increased stress [15–17]. An overall deterioration in body condition can in turn lead to a decrease in immune defence [18–20]. Social factors associated with dispersal, such as loss of social rank and loss of benefits rendered by group membership (e.g., secured foraging territory and anti-predator vigilance), may further exacerbate morphological and physiological costs of dispersal [21,22].

Due to the difficulties of following wide-ranging individuals in the wild, quantification of morphological and physiological costs of dispersal has proven challenging, and there have been only a few such studies on vertebrates. For example, in the red squirrel (*Tamiasciurus hudsonicus*), where juveniles make temporary forays outside the natal territory prior to

emigration, no strong relationship between maximum foray distance and body mass was observed [23]. In the cooperatively breeding pied babbler (*Turdoides bicolor*), lone evicted individuals ("floaters" without territory) lost more body mass than residents due to increased time allocated to vigilance and less efficient foraging [24]. In the cooperatively breeding meerkat (*Suricata suricatta*), where subordinate males undertake extraterritorial prospecting trips [25] and subordinate females are evicted from their natal group [26], both sexes experienced increased stress levels and body mass loss while outside their natal group [16,25,27]. In addition, female meerkats showed reproductive down-regulation [16] and males showed increased testosterone levels [27]. All the above-mentioned studies followed individuals during exploratory movements and early phases of dispersal. Such results are, however, not generalizable among dispersal stages, because disperser candidates are often young and inexperienced and exploratory movements are typically carried out close to the natal range [16,28].

Social species may be able to alleviate some of the costs of dispersal by forming multiple-member dispersing coalitions [29–31], and in many cooperative breeders, subordinate helpers disperse in multiple-member coalitions [13,32–34]. Larger coalitions are likely to experience reduced individual predation risk [30,35], have increased competitive ability [36–38], and faster group-size augmentation, as having more helpers increases reproductive success [31]. Dispersing in larger coalitions may also reduce deterioration in body condition. For example, meerkats that left their natal group in larger coalitions had higher hourly foraging mass gain and lower parasite loads and stress levels [38]. However, how body condition changes with varying coalition size during the entire dispersal event has not yet been formally tested.

Meerkats live in groups of 2–50 individuals and groups are characterized by the presence of a dominant pair that monopolises reproduction [26,39]. During her pregnancy, the dominant female often evicts one or multiple subordinate females [16,26]. When several females are evicted simultaneously, they usually form same-sex multiple-member dispersing coalitions

[26]. After eviction, females remain within the territory of the natal group for a variable period (hereafter referred to as the "post-eviction stage"). At the end of this period, individuals are either accepted back to the natal group as "returners", or permanently emigrate and enter transience as "emigrants". Emigration is here defined as the time when emigrants leave the natal territory and enter transience. Returners do not leave the natal territory nor enter the transient stage [40]. Evicted females' decision to return or emigrate is dependent on a multitude of factors such as natal group size, age, rainfall, population density, coalition size, and availability of unrelated males from other groups [40,41].

In this study, we explore the morphological and physiological costs of dispersal throughout the entire dispersal process from the eviction of subordinate female meerkats until either establishment of a new group or return to the natal group. As such, we extend previous studies by comparing dispersers that successfully settled to dispersers that returned, and by formally assessing costs during the transient stage. We specifically investigate (1) how the loss in body mass and faecal glucocorticoid metabolite levels vary among emigrants, returners, and resident subordinates; and (2) how these measures change between emigration and transient stages. We further investigate (3) how these changes vary with the size of the dispersing coalition while controlling for additional individual and environmental factors.

## METHODS

We conducted our study between September 2013 and March 2017 at the Kalahari Meerkat Project (KMP) located on the Kuruman River Reserve (26° 59' S, 21° 50' E), South Africa. The region is characterized by low seasonal rainfall between October and April and large daily and seasonal temperature variations [26]. Temperature and precipitation data were collected at on-site weather stations.

*GPS data collection and definition of dispersal stages*

We fitted lightweight GPS radio-collars (<25 g, ~3.5% of body mass) on subordinate females a few days prior to, or immediately after, eviction from their natal groups. The collars were composed of a VHF module (Holohil Systems Ltd., Canada) and a GPS module (CDD Ltd., Greece). Collars of this size and weight do not affect meerkat behaviour and survival [42], and we did not observe any sign of distress in animals carrying collars. Typically, only one individual in each dispersing coalition was fitted with a radio-collar. To mount the collars, we sedated individuals using a mixture of isoflurane and oxygen in compliance with the KMP protocol and in collaboration with trained project staff [42]. All necessary permits to handle and tag meerkats were granted to the KMP by the Department of Environment and Nature Conservation of the Northern Cape, South Africa, and the Animal Ethics Committee of the University of Pretoria (permit 'FAUNA 192/2014'). We set the collars to automatically record and store GPS locations at hourly intervals during daytime [43]. However, due to miniaturization of the GPS antenna, we observed a considerable amount of missing GPS fixes.

We used the net squared displacement (NSD) approach, which is stable against missing GPS fixes, to identify time of emigration and time of settlement. The NSD measures the square of the Euclidean distance from the place of eviction to any given GPS location along the dispersal path [44]. By visually investigating the NSD plots of each dispersal event, we identified the inflection points [45], which corresponded to time of emigration and time of settlement (Supplementary material: Figure S1). We further used field observations to validate the NSD approach.

*Field observations*

We located collared dispersing females by means of VHF radio-tracking every two to seven days. Study animals were part of the long-term research at the KMP and were habituated to the presence of humans [46]. At each visit, we recorded dispersing coalition size, number of

associated unrelated males from other groups, and pregnancy status, and we measured individual body mass and collected faecal samples for stress hormone metabolite analysis (see below for more details). To compare dispersers (emigrants and returners) to resident females, we included data collected on same-age subordinate females that resided in the dispersers' respective natal groups (hereafter referred to as "residents").

Resident groups were located by means of VHF radio-tracking (one individual per group was carrying a radio-collar) several times each week by volunteers working at the KMP, and data on group size and composition, female pregnancy status, body mass, and faecal samples were collected. Information on birth date and relatedness of each individual (i.e., dispersers and resident) were available from the long-term database. We considered data on resident individuals for the exact period during which dispersers were absent from the group.

*Determination of body mass*

Individuals in our study population were trained to stand on an electronic balance [46]. We weighted dispersing females at each visit, either in the morning before foraging started or in the evening after foraging ended. To match mass measures collected in the evening and morning, we subtracted the average overnight mass loss (28 g for dispersers) from evening masses and treated them as morning masses on the following day. We calculated average overnight mass loss by subtracting evening and morning masses of dispersers for which consecutive measures were available. Morning measures for resident females were more abundant as resident groups were visited five times per week, and therefore, morning measures alone were sufficient for residents. We excluded from the analyses mass data from pregnant females between the day of conception and the day of parturition or abortion. We determined pregnancy onset by backdating 28 days from the first evidence of abdominal swelling [47,48]. We identified parturition and abortion from a sudden change in abdominal shape and mass loss. After filtering data, we had 192 mass measurements from 25 emigrants, 200 from 28 returners, and 504 from 49 resident subordinates.

*Faecal glucocorticoid metabolite (fGCM) analysis*

We opportunistically collected faecal samples for fGCM analysis immediately after defecation and assigned them to identified individuals. The average time lag between a perceived stressor and its reflection in altered meerkat fGCM concentrations is about 24 hours [49] and we therefore did not collect faecal samples within 2 days after collar deployment. We kept collected samples in insulated thermal bags filled with ice packs until the samples were frozen at -80°C within three hours from collection. Overall, we collected 125 samples from 32 emigrants, 113 samples from 25 returners, and 111 samples from 47 resident subordinates. For steroid extraction, we lyophilized and pulverized faecal samples, and subsequently extracted 0.10-0.11 g of faecal powder with 3 ml of 80 % watery methanol [50]. We subsequently analysed faecal extracts for immunoreactive glucocorticoid metabolite concentrations using a group-specific enzyme immunoassay (EIA) for the measurement of 11ß-hydroxyetiocholanolone [51]. The assay has previously been validated for assessing glucocorticoid output in captive meerkats [49] and has recently been applied successfully to study adrenocortical activity of wild meerkats [52]. Details on assay performance and characteristics, including full descriptions of the assay components and cross-reactivities are provided elsewhere [51,53]. The sensitivity of the EIA at 90 % binding was 0.6 pg. Intra- and inter-assay coefficients of variation of high- and low-value quality controls were 6.2 % (high) and 8.1 % (low) and 7.3 % (high) and 8.7 % (low), respectively. All fGCM concentrations are expressed as hormone mass per dry faecal mass.

*Statistical modelling*

We used linear mixed effects models to analyse variation in (*1a*) body mass loss and (*1b*) fGCM concentration among emigrants, returners, and residents. We used two additional models to compare (*2a*) body mass loss and (*2b*) fGCM concentration between post-eviction (time between eviction and emigration) and transient (time between emigration and settlement)

stages. For models 2a and 2b we only used data collected on emigrants. We conducted all statistical analyses using the library *lme4 [54]* in the software R [55]. We used the library *MuMin [56]* to test different combinations of individual, social, and environmental variables using model selection based on Akaike's Information Criterion [57]. Details for all full models and model parameters are given in the supplements (Tables S1-S4), details of the most parsimonious models are given in the main text (Table 1). To ensure that predictor variables were not correlated with each other, we calculated variance inflation factors [58] for coefficients in the full models. We standardised continuous variables across all data points used for a given model by subtracting their mean and then dividing by their standard deviation. We created residuals plots (Figure S2) and investigated them visually to ensure that model assumptions were met; we did not find any considerable departure from theoretical expectations. Additionally, for each female, we obtained autocorrelation function plots from model residuals to test for temporal autocorrelation [59]. Model residuals showed minor autocorrelation in 3.8 % of the cases and we therefore did not consider temporal autocorrelation as reason for concern.

*1a) Body mass in emigrants, returners, and residents:* We compared the daily proportional change in body mass of emigrants to those of returners and residents. We used a proportional rather than absolute mass change because a given mass loss (or gain) in a light individual would not be equivalent to the same mass loss (or gain) in a heavy individual. Because mass data were collected opportunistically, time between mass measures varied considerably and ranged from 1–81 days (average: 3.21 days, interquartile range: 1–4 days). As we could not assume linearity in mass change across time, we could not reliably and consistently calculate a typically used daily growth rate. Instead, we used a net proportional daily growth rate since eviction $(m_t\text{-}m_0)/(m_0*\Delta t)$, where $m_0$ is the mass at eviction and $\Delta t$ is the number of days elapsed between eviction and a given mass measure $m_t$. Because we were interested in comparing emigrants, returners, and residents, we included a categorical variable

(*strategy*) with these three levels. As larger individuals usually have higher metabolic rates and may lose proportionally more of their body mass [60], we added mass at eviction $m_0$ as an explanatory variable. We treated $m_0$ as a surrogate for body condition because we could not measure body size in the field. We also included the number of days since eviction ($\Delta t$) to investigate if time away from the group influenced mass loss. We included both *age* and $age^{1/2}$ to account for known nonlinearity in meerkat growth [61]. We included a continuous variable *(#female*) indicating the average number of females in a coalition. The reason for averaging being that only 29% of the coalitions changed in size and such changes were of only ±1 individual in most cases. Without averaging, these coalitions would have had a disproportionate high weight in the model output. We added additional covariates, which are known to influence mass of meerkats: number of nutritionally dependent offspring younger than three months in the relevant group *(#pup*), maximum daily temperature (*temp*), and cumulative amount of rain during three months prior to mass measurements (*rain*, [61]). We assigned a unique coalition ID to each dispersal event, and resident individuals that were in dispersers' respective natal group during a given dispersal event.

We treated individual (*indID*) nested in coalition (*coalID*) as the random intercept terms, to account for consistency across repeated measures. Because *coalID* was specific to a given year and therefore partially captured the year effect, we did not include year as a random term to avoid overfitting. Finally, as we observed a large amount of between-individual variation (see Tables S1-S4), we also explored within-individual variation using random slope terms for $m_0$ and *time*. However, due to the low amounts of variation explained by the random slope terms and due to model convergence issues, we decided to use intercept-only terms. The same applies to the models described below.

*1b) fGCM in emigrants, returners, and residents:* The distribution of fGCM levels was right-skewed, and we used *log(fGCM)* as response variable in order to assess differences in stress hormone levels between emigrants, returners, and residents. As described above, we

included *strategy* as well as *Δt, age*, *temp*, *rain*, *#female*, and *male* as explanatory variables. Faecal GCM concentration can vary during the day [49] and between pregnant and non-pregnant females [62]. We accounted for this variation by incorporating two fixed binary variables: sample collected during morning hours (5-12:00) vs. sample collected in the afternoon (15-20:00, *collect*) and female pregnant vs. not pregnant (*preg*). As above, we treated *indID* nested in *coalID* as random intercept terms.

*2a) Emigrant body mass during dispersal stages:* In this analysis, we focused solely on emigrants, ignoring returners and residents, as we were interested in the effect of dispersal stage, which is not available for returners and residents. As above, we used $(m_t\text{-}m_0)/(m_0*\Delta t)$ as response variable and incorporated $m_0$ as a fixed explanatory variable. To investigate the differences in mass loss between dispersal stages, we included a binary variable indicating post-eviction and transience stage (*stage*). Here, *Δt* was the time elapsed since the start of the respective dispersal stage. In contrast to the first model, we removed the variable *#pup* because no pups were present during dispersal. We further included a binary variable (*male*) indicating if at least one unrelated male had joined the coalition. For the rest, we included the same explanatory variables used in the first model: *age*, $age^{1/2}$, *temp*, *rain*, and *#female*. *IndID* was nested in *coalID* as random intercept terms.

*2b) Emigrant fGCM during dispersal stages:* As above, we only used data on emigrants. We used *log(fGCM)* as response variable and included the variables *stage*, *collect*, *preg*, *Δt*, *age*, *temp*, *rain*, and *#female*. We treated *indID* nested in *coalID* as random intercept terms.

**RESULTS**

Females were evicted from their natal groups either alone (n = 33) or as several females at a time forming same-sex dispersing coalitions (n = 32) that varied in size from two to six related females (19 two-, 7 three-, 3 four-, 2 five-, and 1 six-member coalition). On the day of eviction, females were between nine months and five years of age. After eviction, emigrants (n

= 26) dispersed for an average period of 41 days (interquartile range: 13–65 days) before they settled, and returners (n = 39) spent an average period of 24 days (7–30 days) away from their natal group.

*1a) Body mass in emigrants, returners, and residents:* At eviction, emigrants were heavier (716 g ± 21 SE) than returners (672 ± 26 g, ANOVA: $p < 0.001$) and resident subordinates (585 ± 15 g, $p < 0.001$). Based on model predictions (model *1a*, Table 1), emigrants had an average negative daily growth rate (-0.08 % of body mass = -0.60 ± 1.21 g), whereas resident subordinates (0.14 %, 0.82 ± 0.68 g) and returners (0.08 %, 0.53 ± 0.90 g) had a positive growth rate. Daily growth rates decreased with increasing initial body mass, and the effect of initial body mass was strongest in returners (Est = -0.003, SE = 0.001, p = 0.007; Figure 1A, Table 1). Young females gained body mass disproportionately faster than old females (nonlinear age effect: Est = 0.002, SE = 0.001, p = 0.013). Females in larger coalitions lost more mass (Est = -0.002, SE = 0.001, p = 0.032), and they lost body mass faster at high temperatures (Est = -0.001, SE = 0.0002, p = 0.008). Growth rates remained constant throughout the entire dispersal event.

*1b) fGCM in emigrants, returners, and residents:* Faecal GCM levels varied among dispersal strategies. Emigrants and returners experienced overall similar fGCM levels (Est = -2.23, SE = 0.17, p = 0.185) that were on average higher than those of residents (Figure 1B, Table 1). Faecal GCM levels increased with time after eviction (Est = 0.19, SE = 0.07, p = 0.007) and with number of females present in the dispersing coalition (Est = 0.15, SE = 0.08, p = 0.067). Faecal GCM levels decreased with increasing daily temperatures (Est = -0.23, SE = 0.07, $p < 0.001$).

*2a) Emigrant body mass during dispersal stages:* Mass loss of emigrants did not vary between post-eviction and transience, nor with coalition size or presence of unrelated males (Table 1). Mass at eviction had a negative effect on changes in emigrant body mass (Est = -

0.003, SE = 0.001, p = 0.034). Time spent in a dispersal stage did not influence emigrant body mass (Table 1).

*2b) Emigrant fGCM during dispersal stages:* Faecal GCM levels of emigrants varied among dispersal stages (Figure 2) but did not depend on the time emigrants spent in a stage (Table 1). Emigrant females had higher fGCM levels during transience than during post-eviction (Est = 0.37, SE = 0.16, p = 0.024). Dispersing coalition size and presence of males did not affect fGCM levels (Table 1).

## DISCUSSION

Our study emphasizes that dispersal is a costly process and that costs vary between dispersal strategies and dispersal stages. Dispersing females who successfully settled lost body mass, thus confirming the expectation that loss of body mass is associated with dispersal [3]. We further showed that the negative effect of mass at eviction on daily growth rates was more pronounced in dispersers that returned to their natal group than in dispersers that successfully settled in a new territory. Finally, we showed that dispersing females experienced higher faecal glucocorticoid metabolite (fGCM) levels than their resident counterparts, especially in the later stages of dispersal. Our findings thus provide empirical support for the prediction that dispersal is associated with increased stress hormone levels [3].

The fact that dispersers that successfully settled (i.e., emigrants) were on average heavier (also reported in [41]) and less affected by the negative effect of mass at eviction than dispersers that returned to their natal group (i.e., returners), suggests that heavier individuals cope better than lighter individuals when away from the natal group. In actively dispersing species (e.g., birds and mammals), heavier individuals or individuals in better condition often have an advantage during dispersal as they can move faster and further away from the natal territory [63,64]. This increases the likelihood of finding less-saturated territories to settle and to increase breeding opportunities [2,65]. In returners, we did not observe loss of body mass

during the time they spent away from the group. This is in line with a study on red squirrels showing that individuals experience only minor changes in body mass during temporary forays around the natal site [23]. While individuals roaming through familiar areas close to the natal territory are likely to maintain their condition, permanent dispersers may suffer from inefficient foraging in unknown areas [11]. Based on the observed differences in growth rates between emigrants and returners, conclusions regarding a successful dispersal process should be drawn very carefully when based only on prospecting individuals.

The stronger negative effect of body mass at eviction on growth rates of returners may be due to their inexperience of being outside of the group. Over the first years of their life, subordinate females are generally evicted several times before they finally emigrate and establish their own group [26]. During these early evictions, young females can gain information on their surroundings (N. Maag, *pers. obs.*). Similar pre-dispersal movements are common in many species as individuals can gain information on mate availability or quality of future breeding habitat [66,67]. Pre-dispersal forays can thus reduce the costs of dispersal and improve settlement success [28,68]. We propose that lighter and less experienced individuals may not be able to survive dispersal and settle successfully, but that they collect information essential for future dispersal.

Contrary to expectations [3,24], we did not observe a decrease in growth rate with increasing dispersal time nor with time spent in a dispersal stage [3,24]. Hence, the energetic costs of being away from the group may not be as high as previously thought [3,11]. However, to assess the influence of dispersal on body condition, an investigation of cumulative distance covered by each individual could be more informative [3]. While we incorporated cumulative distance in earlier models, we then removed it because the models were not robust. This was probably due to the considerable amount of missing GPS fixes, which resulted in inaccurate cumulative distance measures. We suggest that future studies should explore the influence of dispersal distance on changes in individual body mass and stress levels.

We further confirm previous results showing that mass loss in dispersing meerkats can be alleviated in larger coalitions [38]. Since cooperative birds and mammals can partition cooperative behaviour like vigilance among group members [69,70], dispersing in larger coalitions is likely to reduce the individual costs of such behaviour during dispersal. This allows individuals in larger coalitions to allocate more time to foraging [38,69,70]. If increased foraging time in larger coalitions buffers against daily individual mass loss, our results may apply to many cooperative species that disperse in multiple-member coalitions such as lions (*Panthera leo*), wild dogs (*Lycaon pictus*), green woodhoopoes (*Phoeniculus purpureus*), or Arabian babblers (*Turdoides squamiceps*) [13,32–34]. In addition, individuals in larger coalitions may have an advantage as they can establish a new breeding unit with a larger initial group size. Starting a new group with several helpers will likely increase total group reproduction and survival of individuals due to improved group augmentation [71,72]. Coalition size did have no effect on body mass when investigating solely emigrants, which may be explained by the low availability of data for large coalitions.

Aggression from the dominant female during eviction and the lack of protection offered by the group after eviction may be responsible for the higher fGCM levels during the post-eviction stage [16]. Aggressive attacks are used by dominants of several cooperative species to render their subordinates infertile through chronic stress [73,74] and are a likely explanation for increased fGCM concentrations in meerkats [16]. Changes in physical and social environment associated with dispersal, such as unfamiliarity with the landscape and aggression from unrelated residents, are likely to intensify during transience and offer an explanation for the increased stress hormone levels during this stage of the dispersal process [75,76]. Many species cope with unpredictable stimuli by exhibiting a stress response, which may lead to increased glucocorticoid levels [6]. Increased glucocorticoid levels as response to homeostatic challenges are at first place adaptive [77]. Only when stress hormones are elevated over

prolonged periods (i.e., chronically) they have deleterious impacts on an individual's fitness [78]. As such, the observed change in fGCM concentrations may be an adaptive response to the challenge of dispersal rather than a real cost of affecting fitness negatively. However, if individuals are unable to find suitable territory for settlement in time, chronic stress may lead to decreased fitness later in life [76].

Unexpectedly, and in contrast to previous work by Young [38], we observed not a reduction but an increase of stress hormone levels in females of larger coalitions. This difference is possibly due to the fact that Young [38] focused mainly on the early phases of dispersal. In other species, glucocorticoid levels of reproductive competitors increase during times of social instability [79,80] and such instability is likely to occur during the late stages of dispersal, when individuals establish new breeding groups. As aggression and reproductive conflict increase with group size in social species [82,83], increased reproductive competition in larger coalitions may increase individual stress hormone levels. Our results suggest that social circumstances can change during the dispersal process and cause variation in fGCM concentrations.

In conclusion, we show that dispersing females who successfully settle experience greater mass loss than resident females and evicted females who return to the natal group. Both emigrants and returners have higher stress hormone output than residents, especially during the later stages of dispersal. We thereby confirm previous findings, but also extend those by showing how body condition varies between different female strategies and dispersal stages. Body mass and stress hormone output seem suitable parameters for monitoring the costs associated with dispersal, as these traits often play an important role in mediating the effects of the environment on other life-history events such as survival and breeding [7–9]. A better quantification of how such costs change in response to social and environmental conditions across different stages of dispersal can therefore help gain a better mechanistic understanding of this important life history event. As many vertebrate species are expected to experience

condition loss during dispersal [2,3], our results – showing how body condition changes during the later stages of dispersal – should hold implications for a wide range of taxa. Quantification of the effects of dispersal on individual condition will permit a trait-based investigation of the associated demographic rates and how these affect population dynamics.

## ACKNOWLEDGEMENTS

Funding for this study was provided by the Swiss National Science Foundation (Project CR32I3_159743). We thank the Northern Cape Conservation Authority for permission to conduct this research, and the farmers neighbouring the Kuruman River Reserve for granting us access to their private lands. We thank the field managers and volunteers for facilitating field work and helping with data collection, in particular David Gaynor and Tim Vink. Special thanks go to our field assistants David Seager, Ana Morales González, Héctor Ruiz Villar, Peter Clark, Luc Le Grand, Louis Bliard, Natasha Harrison, and Frances Mullany. We thank Stefanie Ganswindt for hormone extraction and Andrea Heistermann for hormone analysis. We thank Luca Börger for fruitful discussions and comments on the manuscript, and Tina Cornioley and Mollie Brooks for their help with statistical analyses. Our research relied on records of individual identities and life histories of meerkats, and research facilities maintained by the Kalahari Meerkat Project, which has been supported by the European Research Council (Research Grant No 294494 to T.H. Clutton-Brock), the University of Zurich and the Mammal Research Institute at the University of Pretoria.

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## FIGURES AND TABLES

*Figure 1.* Effects of (A) initial body mass at eviction on net proportional daily change in body mass, and (B) dispersing coalition size on faecal glucocorticoid metabolite (fGCM) concentration in female meerkats. A) Points show average daily mass changes for each female with standard errors. The lines show model predictions for each female strategy (resident, returner, emigrant) when all other model predictors were set to their mean. B) Points show observed fGCM concentrations and lines show model predictions for each female strategy when all other model predictors were set to their mean. The slopes capture the change in the response for a one-standard-deviation increase in the respective variable. Significance values are given in Table 1.

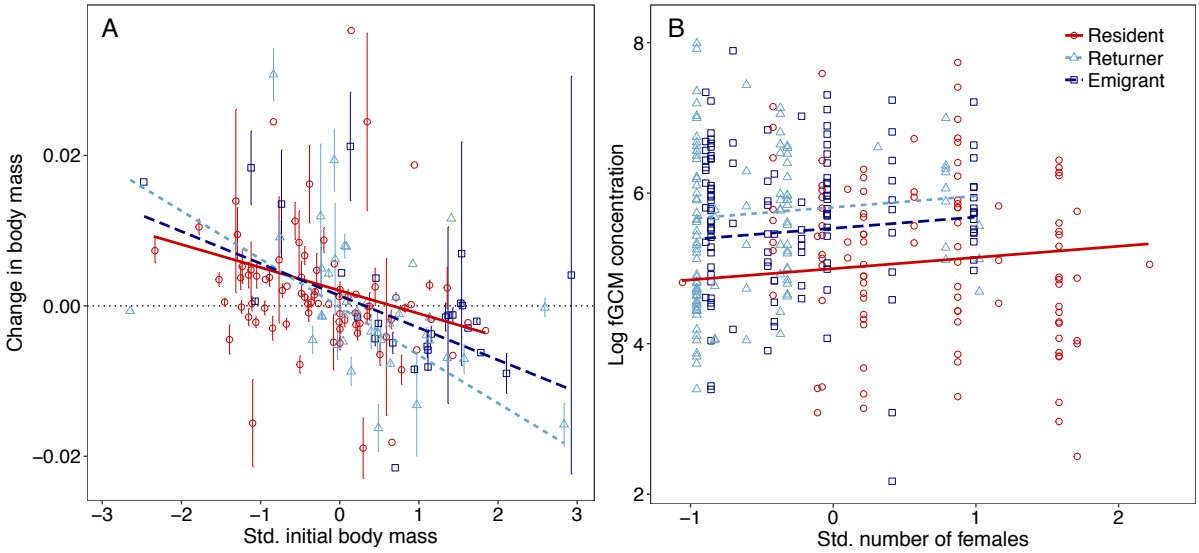


*Figure 2.* Faecal glucocorticoid metabolite (fGCM) concentrations in female meerkat emigrants depending on whether they were in the post-eviction or transience stage. Empty symbols show observed fGCM concentrations and filled symbols show model estimates with 95% confidence intervals.

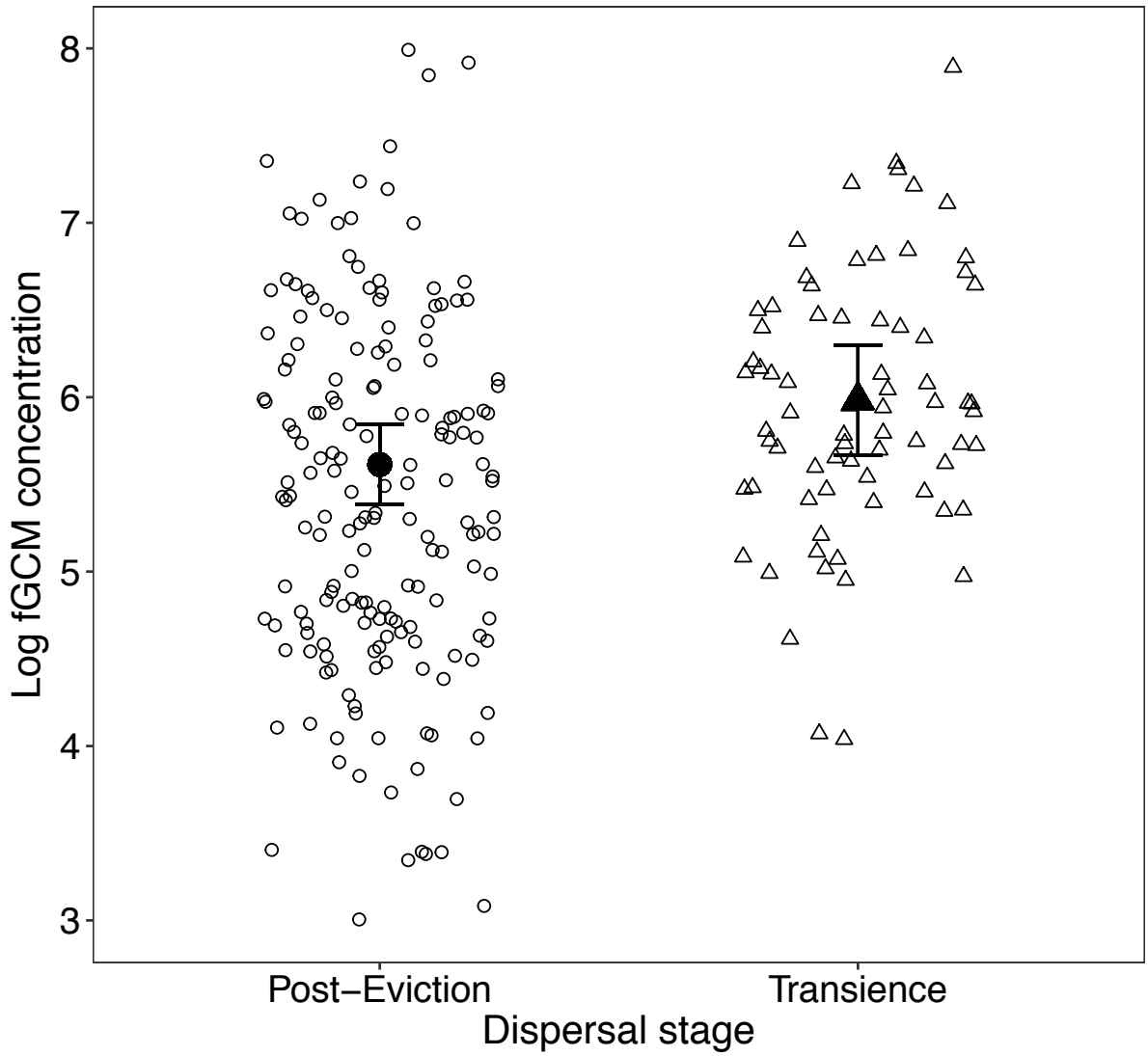


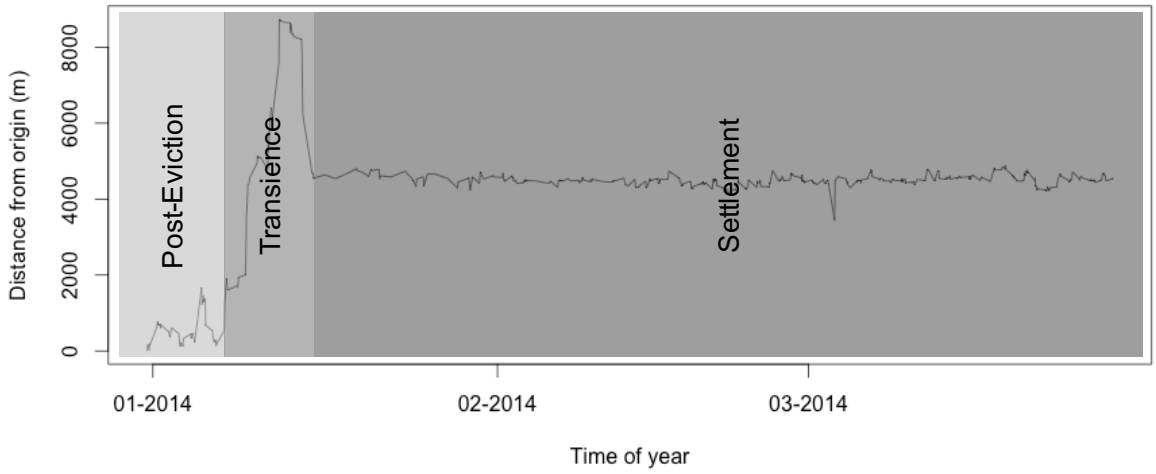
*Table 1.* Effects of individual, social, and environmental factors on net proportional daily changes in body mass and faecal glucocorticoid metabolite (fGCM) concentrations of female meerkats included in final models (top row). The estimate (Est) and standard error (SE) from the final model are reported for each term, as is the effect of removing each term from the final model (minus signs) on the model degrees of freedom (df) and Akaike's Information Criterion for small sample sizes (ΔAICc). Interaction effects were taken away when either of the single effects were removed (denoted in brackets). Significance (p) is based on Wald statistics. Marginal $R^2$ represents the variance explained by fixed factors ($R^2_m$), and conditional $R^2$ represents the variance explained by both fixed and random factors ($R^2_c$). The explanatory variables are $m_0$ = initial mass, $age^{1/2}$ = sqrt of age to account for nonlinearity in growth, *temp* = max daily temperature, *#female* = average number of females, *strategy* = emigrants vs. returners vs. residents, *collect* = sample collected am or pm, *preg* = female pregnant or not, $\Delta t$ = days since eviction, and *stage* = post-eviction vs. transience.

| Model | Est | SE | p | df | ΔAICc |
|---|---|---|---|---|---|
| 1a) Body mass in emigrants, returners, and residents | | | $R^2_m$=0.12, $R^2_c$=0.71 | | |
| *$m_0$+age$^{1/2}$+temp+#female+strategy+ $m_0$:strategy* | | | | 12 | 0 |
| *- strategyReturner (-$m_0$:strategy)* | -0.001 | 0.001 | 0.675 | 8 | 1.14 |
| *- strategyEmigrant (-$m_0$:strategy)* | 0.000 | 0.002 | 0.911 | | |
| *- #female* | -0.002 | 0.001 | 0.032 | 11 | 2.67 |
| *- $m_0$:strategyReturner* | -0.003 | 0.001 | 0.007 | 10 | 3.53 |
| *- $m_0$:strategyEmigrant* | -0.001 | 0.001 | 0.342 | | |
| *- age$^{1/2}$* | 0.002 | 0.001 | 0.013 | 11 | 4.5 |
| *- temp* | -0.001 | 0.000 | 0.008 | 11 | 5.02 |
| *- $m_0$ (-$m_0$:strategy)* | -0.003 | 0.001 | 0.002 | 9 | 34 |
| 1b) fGCM in emigrants, returners, and residents | | | $R^2_m$=0.15, $R^2_c$=0.28 | | |
| *collect+preg+Δt+temp+#female+strategy* | | | | 11 | 0 |
| *- #female* | 0.149 | 0.081 | 0.067 | 10 | 1.3 |
| *- Δt* | 0.185 | 0.068 | 0.007 | 10 | 5.34 |
| *- temp* | -0.232 | 0.065 | <0.001 | 10 | 9.9 |
| *- strategyReturner* | 0.772 | 0.191 | <0.001 | 9 | 13.47 |
| *- strategyEmigrant* | 0.542 | 0.170 | 0.002 | | |
| *collectPM* | -0.404 | 0.111 | <0.001 | | fixed |
| *pregPregnant* | 0.152 | 0.127 | 0.234 | | fixed |
| 2a) Emigrant body mass during dispersal stages | | | $R^2_m$=0.07, $R^2_c$=0.65 | | |
| *$m_0$* | | | | 5 | 0 |
| *- $m_0$* | -0.003 | 0.001 | 0.034 | 4 | 1.8 |
| 2b) Emigrant fGCM during dispersal stages | | | $R^2_m$=0.09, $R^2_c$=0.22 | | |
| *collect+preg+stage* | | | | 7 | 0 |
| *- stageTransience* | 0.369 | 0.162 | 0.024 | 6 | 2.99 |
| *collectPM* | -0.465 | 0.129 | <0.001 | | fixed |
| *pregPregnant* | 0.044 | 0.146 | 0.766 | | fixed |

## SUPPLEMENTARY INFORMATION

**Figure S1.** Net displacement curve of dispersing meerkats

Characteristic dispersal curve of a dispersing coalition of female meerkats quantified by net displacement (distance to natal site). The post-eviction phase starts after the eviction event and is characterized by typical territorial movement patterns, where coalitions remain in the natal territory and distances covered per day resemble those of the natal group. Emigration marks the beginning of transience, where coalitions cover farther distances per day and move away from the natal site. The time of settlement can clearly be identified by a change to territorial movement patterns.



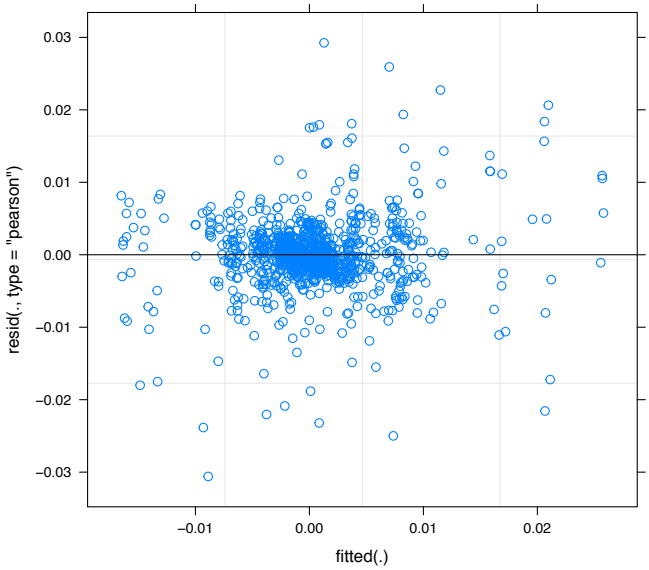

Variations in NSD over time can be used to characterize transitions from one dispersal stage to the next. For each dispersing coalition, we calculated the NSD as the square of the Euclidean distance from the place of eviction to any given GPS location along the entire dispersal path. We then visually investigated the resulting NSD plots for inflection points (Cozzi et al. 2016)[5], which corresponded to time of emigration and time of settlement. We used field observations

[5] Cozzi G, Chynoweth M, Kusak J, Çoban E, Çoban A, Ozgul A, Şekercioğlu ÇH. 2016 Anthropogenic food resources foster the coexistence of distinct life history strategies: year-round sedentary and migratory brown bears. *J. Zool.* **300**, 142–150.

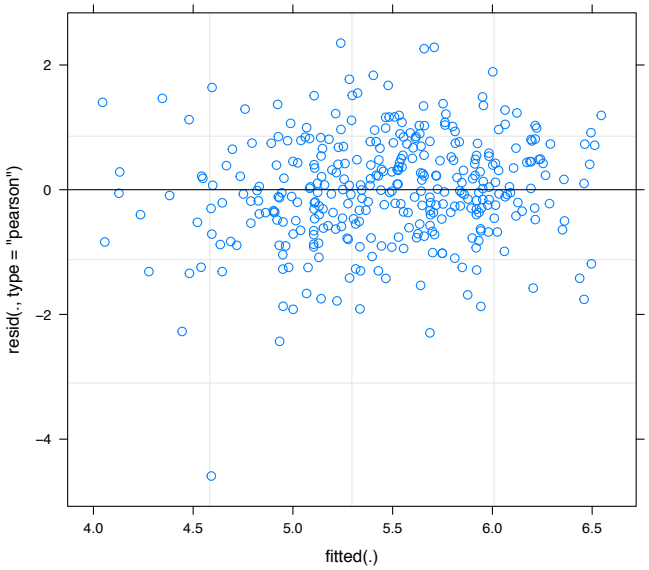
to validate results from the NSD approach. Successful emigration was typically characterized by unidirectional exploratory movements and lack of attempts to reunite with the natal group. Successful settlement coincided with the use of the same sleeping burrow for extended periods (>1 week) accompanied by normal foraging behaviour resembling territorial behaviour.

**Figure S2.** Residuals diagnostics for statistical models

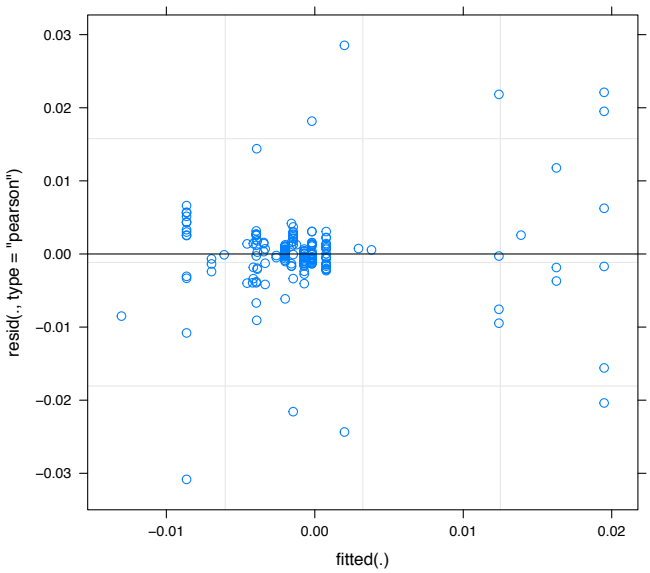
Linear mixed effects **model *1a***: Comparison of net proportional daily mass change among emigrants, returners, and residents.




Linear mixed effects **model *1b***: Comparison of faecal glucocorticoid metabolite (fGCM) concentrations among emigrants, returners, and residents.



Linear mixed effects **model *2a***: Variation in net proportional daily mass change between post-eviction and transience stages in emigrants.




Linear mixed effects **model *2b***: Variation in faecal glucocorticoid metabolite (fGCM) concentrations between post-eviction and transience stages in emigrants.

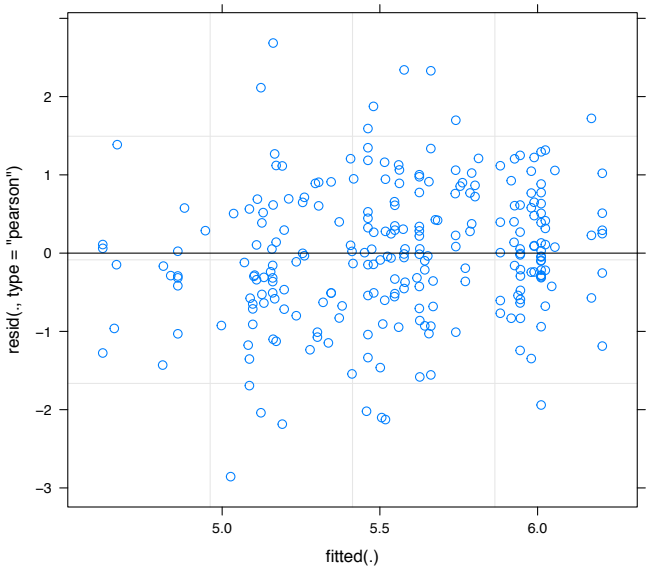


**Table S1.** Linear mixed effects model *1a*: Comparison of net proportional daily mass change among emigrants, returners, and residents.

**Upper table:** Description of full statistical model. **Lower table:** Ten best models from model selection based on Akaike's information criterion; DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model based on AICc; W = Akaike weights.

| Response | Fixed | Variable description | Random |
|---|---|---|---|
| $(m_t-m_0)/(m_0*\Delta_t)$ | $m_0$ | Body mass at day of eviction | *indID* |
| | $\Delta t$ | Days since eviction | nested in |
| | *age* | Age in months | *coalID* |
| | $age^{1/2}$ | Account for non-linear growth of individuals <2 years | |
| | *rain* | Rain sum of previous 3 months | |
| | *temp* | Maximum daily temperature | |
| | *#pup* | Number of dependent offspring <3 months age | |
| | *strategy* | Female strategy; Factor: Resident, Returner, Emigrant | |
| | *#female* | Average number of females in group, dispersing coalition, respectively | |
| | *strategy:#female* | | |
| | $strategy:m_0$ | | |

| Variable | DF | AICc | ΔAICc | W |
|---|---|---|---|---|
| $m_0+temp+age^{1/2}+\#female+strategy+strategy:m_0$ | 12 | -7519.55 | 0.00 | 0.03 |
| $m_0+temp+age+\#female+strategy+strategy:m_0$ | 12 | -7519.31 | 0.24 | 0.03 |
| $m_0+temp+rain+age^{1/2}+\#female+strategy+strategy:m_0$ | 13 | -7518.77 | 0.78 | 0.02 |
| $m_0+temp+rain+age+\#female+strategy+strategy:m_0$ | 13 | -7518.53 | 1.02 | 0.02 |
| $m_0+\Delta t+temp+age^{1/2}+\#female+strategy+strategy:m_0$ | 13 | -7518.49 | 1.06 | 0.02 |
| $m_0+\Delta t+temp+age+\#female+strategy+strategy:m_0$ | 13 | -7518.42 | 1.13 | 0.02 |
| $m_0+temp+age^{1/2}+\#female$ | 8 | -7518.42 | 1.14 | 0.02 |
| $m_0+temp+age^{1/2}+\#female$ | 8 | -7518.27 | 1.28 | 0.02 |
| $m_0+temp+age+\#female+strategy+strategy:m_0+strategy:\#female$ | 14 | -7518.20 | 1.35 | 0.02 |
| $m_0+\Delta t+temp+rain+age^{1/2}+\#female+strategy+strategy:m_0$ | 14 | -7518.15 | 1.40 | 0.02 |

**Table S2.** Linear mixed effects model *1b*: Comparison of faecal glucocorticoid metabolite (fGCM) concentrations among emigrants, returners, and residents.

**Upper table:** Description of full statistical model. **Lower table:** Ten best models from model selection based on Akaike's information criterion; DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model based on AICc; W = Akaike weights.

| Response | Fixed | Variable description | Random |
|---|---|---|---|
| *log(fGCM)* | *collect* | Collection time; Factor: Morning, Afternoon | *indID* |
| | *preg* | Pregnancy; Factor: 1 = Pregnant, 0 = Not pregnant | nested in |
| | *Δt* | Days since eviction | *coalID* |
| | *age* | Age in months | |
| | *rain* | Rain sum of previous 3 months | |
| | *temp* | Maximum daily temperature | |
| | *strategy* | Female strategy; Factor: Resident, Returner, Emigrant | |
| | *#female* | Average number of females in group, dispersing coalition, respectively | |
| | *strategy:#female* | | |

| Variable | DF | AICc | ΔAICc | W |
|---|---|---|---|---|
| *collect+preg+Δt+temp+#female+strategy* | 11 | 974.23 | 0.00 | 0.25 |
| *collect+preg+Δt+temp+age+#female+strategy* | 12 | 975.28 | 1.05 | 0.15 |
| *collect+preg+Δt+temp+strategy* | 10 | 975.53 | 1.30 | 0.13 |
| *collect+preg+Δt+temp+rain+#female+strategy* | 12 | 976.28 | 2.05 | 0.09 |
| *collect+preg+Δt+temp+age+strategy* | 11 | 976.68 | 2.45 | 0.07 |
| *collect+preg+Δt+temp+rain+age+#female+strategy* | 13 | 977.29 | 3.06 | 0.05 |
| *collect+preg+Δt+temp+rain+strategy* | 11 | 977.69 | 3.46 | 0.04 |
| *collect+preg+Δt+temp+#female+strategy+strategy:#female* | 13 | 978.17 | 3.94 | 0.03 |
| *collect+preg+Δt+temp+rain+age+strategy* | 12 | 978.84 | 4.62 | 0.02 |
| *collect+preg+Δt+temp+age+#female+strategy+strategy:#female* | 14 | 979.05 | 4.83 | 0.02 |

**Table S3.** Linear mixed effects model *2a*: Variation in net proportional daily mass change between post-eviction and transience stages in emigrants.

**Upper table:** Description of full statistical model. **Lower table:** Ten best models from model selection based on Akaike's information criterion; DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model based on AICc; W = Akaike weights.

| Response | Fixed | Variable description | Random |
|---|---|---|---|
| $(m_t-m_0)/(m_0*\Delta_t)$ | $m_0$ | Body mass at day of eviction | *indID* |
| | $\Delta t$ | Days since start of stage (Post-eviction, Transience) | nested in |
| | *age* | Age in months | *coalID* |
| | $age^{1/2}$ | Account for non-linear growth of individuals <2 years | |
| | *rain* | Rain sum of previous 3 months | |
| | *temp* | Maximum daily temperature | |
| | *stage* | Dispersal stage; Factor: Post-Eviction, Transience | |
| | *#female* | Average number of females in dispersing coalitions | |
| | *male* | Male presence; Factor: Male present, Male absent | |
| | *status:#female* | | |

| Variable | DF | AICc | ΔAICc | W |
|---|---|---|---|---|
| $m_0$ | 5 | -1369.66 | 0.00 | 0.06 |
| $m_0$+*stage* | 6 | -1368.63 | 1.03 | 0.03 |
| $m_0$+*temp* | 6 | -1368.21 | 1.45 | 0.03 |
| $m_0$+*rain* | 6 | -1367.87 | 1.78 | 0.02 |
| *Null* | 4 | -1367.86 | 1.80 | 0.02 |
| $m_0$+*#female* | 6 | -1367.82 | 1.84 | 0.02 |
| $m_0$+*male* | 6 | -1367.53 | 2.12 | 0.02 |
| $m_0$+$age^{1/2}$ | 6 | -1367.48 | 2.17 | 0.02 |
| $m_0$+*age* | 6 | -1367.46 | 2.20 | 0.02 |
| *age* | 5 | -1367.23 | 2.43 | 0.02 |

**Table S4.** Linear mixed effects model *2b*: Variation in faecal glucocorticoid metabolite (fGCM) concentrations between post-eviction and transience stages in emigrants.

**Upper table:** Description of full statistical model. **Lower table:** Ten best models from model selection based on Akaike's information criterion**;** DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model based on AICc; W = Akaike weights.

| Response | Fixed | Variable description | Random |
|---|---|---|---|
| *log(fGCM)* | *collect* | Collection time; Factor: Morning, Afternoon | *indID* |
| | *preg* | Pregnancy; Factor: 1 = Pregnant, 0 = Not pregnant | nested in |
| | *Δt* | Days since start of stage (Post-eviction, Transience) | *coalID* |
| | *age* | Age in months | |
| | *rain* | Rain sum of previous 3 months | |
| | *temp* | Maximum daily temperature | |
| | *stage* | Dispersal stage; Factor: Post-Eviction, Transience | |
| | *#female* | Average number of females in dispersing coalition | |
| | *male* | Male presence; Factor: Male present, Male absent | |
| | *stage:#female* | | |

| Variable | DF | AICc | ΔAICc | W |
|---|---|---|---|---|
| *collect+preg+stage* | 7 | 698.82 | 0.00 | 0.13 |
| *collect+preg+temp+rain+stage* | 9 | 699.16 | 0.34 | 0.11 |
| *collect+preg+rain+stage* | 8 | 699.19 | 0.37 | 0.11 |
| *collect+preg+temp+stage* | 8 | 699.49 | 0.67 | 0.09 |
| *collect+preg+age+stage* | 8 | 700.57 | 1.75 | 0.05 |
| *collect+preg+male+stage* | 8 | 700.90 | 2.08 | 0.05 |
| *collect+preg+#female+stage* | 8 | 701.02 | 2.20 | 0.04 |
| *collect+preg+temp+rain+age+stage* | 10 | 701.11 | 2.29 | 0.04 |
| *collect+preg+rain+age+stage* | 9 | 701.15 | 2.33 | 0.04 |
| *collect+preg+temp+age+stage* | 9 | 701.19 | 2.37 | 0.04 |

# CHAPTER FOUR

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## Group size and male presence affect deposition of scent marks in dispersing female meerkats

*Behavioral Ecology (in review)*

Photo credit: Héctor Ruíz-Villar

# Group size and male presence affect deposition of scent marks in dispersing female meerkats

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**ABSTRACT**

Several animal species use scent marks such as faeces and urine to find mates, advertise their reproductive status, and defend an exclusive territory. Scent marking may be particularly important during dispersal, when individuals emigrate from their natal territory searching for mates and new territory to settle and reproduce. In this study, we investigated scent marking behaviour of 30 dispersing female meerkats (*Suricata suricatta*) during the three consecutive phases of dispersal: emigration, transience, and settlement. We expected patterns of defecation and urination to differ among dispersal phases and depending on social circumstances, but also to be influenced by water and food availability. We showed that defecation increased substantially during the settlement phase, suggesting that dispersers use faeces to signal their presence to secure an exclusive territory. Association with unrelated males increased urination frequency, irrespective of dispersal phase, suggesting that urine may serve as within-group communication channel to advertise social and reproductive status. We did not detect any positive effect of rainfall, a proxy for water and food abundance, on defecation and urination frequency. Our results suggest that faeces may be a long-lasting communication channel and thus may be most suited for between-group communication; while urine may mainly serve as a within-group short-term information transfer.

**Keywords:** Cooperative breeder, chemical signalling, dispersal stage, GPS tracking, radio collar, social rank

## INTRODUCTION

Scent marking plays an important role in mediating mammal communication (Ralls 1971; Thiessen and Rice 1976). Faeces, urine and other glandular secretions contain chemical compounds that provide information about an individual's sex, age, reproductive status and health condition (Stockley et al. 2013; Crawford and Drea 2015). These chemical signals are used for several purposes such as territorial advertisement and maintenance (Peters and Mech 1975; Stewart et al. 2002), sexual communication, mate choice (Thomas 2002; Allen et al. 2015), social communication, and individual identification (Hurst et al. 2001; Leclaire et al. 2013). As such, scent markings are expected to convey different messages, and the rate at which these messages are conveyed is expected to change during different stages of an individual's life.

At present, a major challenge is our inability to unambiguously distinguishing between defecation and urination as simple elimination of metabolic wastes or for scent marking purposes (Jordan et al. 2013). Environmental conditions can be expected to influence defecation and urination (Fornasieri and Roeder 1992; Huynh et al. 2005). Rainfall increases water and food availability (Bergallo and Magnusson 1999; Rimbach et al. 2018), which have been shown to increase the elimination of metabolic waste (Mattson et al. 1991; Murphy 1992), and high temperatures have been shown to negatively affect urination due to increased evaporative loss (Huynh et al. 2005). Besides representing metabolic processes, defecation and urination, particularly their timing and location during active movement, can also vary due to signalling. While we may not know what message is contained in faeces and urine, they inarguably inform about an individual's presence (Hurst et al. 2001; Jordan et al. 2013). An increase (respectively decrease) in defecation and urination rate may thus reflect an individual's readiness to communicate (respectively hide) its presence, beside a series of other individual information (Ralls 1971). We therefore argue that changes in defecation and urination patterns across life-history stages and social situations may be indicative of changes

in scent marking-mediated communication patterns, and thus help identifying the ultimate mechanism of scent marking under different circumstances and life-history stages. It is in this broad context that we hereafter refer to defecation and urination as scent markings.

A key stage in an individual's life is dispersal from the natal territory (Bowler and Benton 2005). Dispersal consists of three phases: emigration from the natal territory, transience through unfamiliar areas, and settlement in a suitable habitat, and each phase depends on different individual, social, and environmental factors (Clobert et al. 2012). In many animal species, dispersal success much depends on the dispersers' ability to find unrelated mates and to locate a vacant territory for settlement, while minimizing predation risk and aggression from conspecifics (Bowler and Benton 2005; Cozzi et al. 2018). At each phase, dispersers thus need to trade-off the costs and benefits of scent marking, because scents may be detected by both target and unwanted receivers (Viitala et al. 1995; Roberts and Gosling 2001). Therefore, scent marking is expected to play a significant role and to change as a function of specific communication purposes – such as mate attraction – as the dispersal process progresses.

During the early phase of dispersal, dispersers often search for unrelated mates (Clobert et al. 2012; Maag et al. 2018), and an increase in scent marking rate may facilitate mate finding by conveying information about own presence, quality and reproductive status (Thomas 2002; Vogt et al. 2014). Hence, scent marking rate can be expected to be high prior to association with unrelated individuals of the opposite sex, as it has been shown for some species such as ocelots (*Leopardus pardalis*) (King et al. 2016), coyotes (*Canis latrans*) (Gese and Ruff 1997), and Carolina anoles (*Anolis carolinensis*) (Jenssen et al. 1995). Following association with mates, however, dispersers may decrease scent markings to reduce predation risk or aggression from conspecifics (Viitala et al. 1995; Bowler and Benton 2005). For example, high-ranking mice (*Mus musculus*) reduce the time spent overmarking intruder's marks to minimise the cost of predation (Roberts et al. 2001). Finally, during the late phase of dispersal, scent marking

rate may increase to advertise the own presence after settlement in a new territory (Roberts and Gosling 2001).

In social species, scent marking also serves as a within-group communication (Jordan et al. 2010), and this may partly overwrite the use of scent markings for between-groups communication purposes. For instance, advertisement of an individual's social status through scent marking can facilitate the maintenance of group cohesion by conveying information about dominance and reproductive status (Hurst et al. 2001; Thavarajah et al. 2014). Scent marking can reduce physical confrontation (Hurst 1990; Rajagopal et al. 2010), as individuals can assess the physical condition of the marking individual and avoid direct fights with stronger opponents, thus reducing injuries (Gosling and McKay 1990). Where individuals disperse in multiple-member coalitions (Lundy et al. 1998; Cant et al. 2001), and coalition members compete for dominance (Clutton-Brock et al. 2006), scent marking may increase with increasing coalitions size, and it can be expected to remain relatively high as long as dominance is unambiguously established.

A long-term study of a wild population of meerkats (*Suricata suricatta*) in the Kalahari Desert (Clutton-Brock and Manser 2016) provides a unique opportunity to study how defecation and urination frequencies change during dispersal. Several aspects of the dispersal behaviour of meerkats (*Suricata suricatta*) have been investigated (Young et al. 2006; Mares et al. 2014), including their movements through a social landscape composed of unrelated territorial groups (Cozzi et al. 2018), the transitioning between different phases of dispersal (Maag et al. 2018), and the physiological costs of dispersal (Maag et al. *in review*). However, little is known about the marking behaviour of dispersing female meerkats (Cozzi et al. 2018) while the importance of marking behaviour in resident groups is well documented and understood (Jordan et al. 2007; Leclaire et al. 2017).

In this study, we investigated patterns of defecation and urination in female meerkats during dispersal. We focused on mornings and evenings, the periods of main activity. We tested

the following three hypotheses: 1) Defecation and urination rates of female dispersers vary among the three phases of dispersal; 2) Females defecate and urinate more in the absence of unrelated males; 3) Females in large dispersing coalitions defecate and urinate more than females in small coalitions.

## METHODS

### *Study site and species*

We conducted our study between September 2013 and April 2017 at the Kalahari Meerkat Project (KMP) located on the Kuruman River Reserve (26° 59' S, 21° 50' E), South Africa, and adjacent farms. The region is characterised by low seasonal rainfall during hot summers between October and April, and dry cold winters (Clutton-Brock et al. 1998). Temperature and precipitation data were available from on-site weather stations.

Meerkats live in groups of up to 50 individuals (Doolan and Macdonald 2009), consisting of a dominant pair that monopolizes breeding and several subordinate individuals (Doolan and Macdonald 1996; Griffin et al. 2003). During her pregnancy, the dominant female evicts one or multiple subordinate females from the natal group (Clutton-Brock et al. 1998). Evicted females remain in the natal territory for a variable time period (hereafter referred to as "post-eviction phase") before they permanently emigrate (hereafter referred to as "departure") and enter the transient phase, or return to the natal group. Evicted females can disperse alone or in same-sex multiple-member dispersing coalitions (Young et al. 2006) and are joined by unrelated males from other groups during the dispersal process (Maag et al. 2018).

### *GPS data collection*

We deployed GPS radio-collars (<25 g, ~3.5 % of meerkat body mass) on subordinate females right before, or immediately after, eviction from the natal group. The radio-collars were composed of a GPS module (CDD Ltd., Greece) and a VHF module (Holohil Systems Ltd., Canada) for radio tracking. We set the collars to record GPS locations during daytime

until and after settlement in a new territory. To deploy the collars, individuals were sedated using a mixture of isoflurane and oxygen following the KMP protocol and assisted by the trained project staff (Jordan et al. 2007). All necessary permits to handle and tag meerkats were granted to the KMP by the Department of Environment and Nature Conservation of South Africa and the Animal Ethics Committee of the University of Pretoria (permit 'FAUNA 192/2014').

*Identification of discrete dispersal phases*

Using the GPS data, we calculated net squared displacement (NSD) trajectories for each dispersal event. The NSD is the square of the Euclidian distance from the origin (the place of eviction in our case) to any given GPS location along the dispersal path, and it can be used to investigate various movement modes, including dispersal (Börger and Fryxell 2012). By visually investigating the NSD plots of each dispersal event, we identified the inflection points (Cozzi et al. 2016), which corresponded to time of departure (transition from post-eviction to transience) and time of settlement (transition from transience to settlement in a new territory). We used field observations to validate results from the NSD approach. Details on the exact method can be found in Maag et al. (2018).

*Behavioural data collection*

We located dispersing coalitions by means of VHF radio-tracking every two to seven days. At each visit, we recorded data on female coalition size, female social status within the coalition, and association with unrelated males. We further recorded individual behaviours, hereafter referred to as focal follows. During a focal follow, which lasted 15 minutes, a specific individual was closely monitored (meerkats were habituated to human presence to within 1 m) and each behaviour, including counting defecation and urination events, was annotated with Cyber Tracker Software (Cyber Tracker Conservation 2013, USA) on common tablet computers (Asus Fonepad 7, ASUSTeK Computer Inc., China). We set the duration of a focal

follow to ensure that no more than one defecation and urination event could take place within each follow. This allowed treating defecation and urination as a binomial response variable (see below). We conducted focal follows within three hours after the meerkats left the sleeping burrow in the morning, and two hours before they returned to the burrow in the evening. These represent the times of main activity, as meerkats typically rest over the hot midday hours (Doolan and Macdonald 1996). We focal followed each study animal 1–3 times per week. If the same individual was followed more than one time on the same day, focal follows were spaced by at least 30 min and assumed to be independent.

*Statistical analysis*

We fitted two generalised mixed effects models with defecation and urination probabilities as binomial response variables respectively. We assigned one of two outcomes to each behavioural focal follow: 0 = no defecation (respectively no urination); 1 = defecation (respectively urination). Of primary interest were the effect of dispersal phase (categorical: post-eviction vs. transience vs. settlement), presence of unrelated males (0 = no male present, 1= at least one male present), and number of females in the dispersing coalition on defecation and urination probabilities. We added cumulative amount of rain during one month prior to the focal follow, and the maximum temperature on the day of the focal follow as additional covariates to account for the effect of environmental conditions (e.g. water and food availability) on defecation and urination rate. We also incorporated biological meaningful interactions term, which are described in the supplementary information (Tables S1-S2). We included individual identity, coalition identity, and year as random terms.

We conducted both statistical analyses with the package *lme4* (Bates et al. 2016) in the software R (R Core Team 2017). We used model selection to test all combinations of the predictor variables. Model selection was based on Akaike's Information Criterion (AIC; Akaike 1973) using the library *MuMin* (Barton 2015). To exclude collinearity among predictor variables, we calculated Variance Inflation Factors (VIF; Belsley et al. 2005) for coefficients

in the full models. Details of model selection are given in the supplementary material (Tables S1-S2). In both models, we standardised continuous variables by subtracting their mean and dividing by the standard deviation.

## RESULTS

We followed 30 females in 18 dispersing coalitions and recorded a total of 527 behavioural focal follows. Of those, 192 were obtained in the post-eviction phase, 106 in the transient phase, and 229 in the settlement phase.

Defecation rate was higher in the absence of unrelated males (Estimate = 0.83, Standard Error = 0.51) in all three dispersal phases (Figure 1, Table S1). There was no difference in defecation rate between the post-eviction and transient phase, while it was higher during the settlement phase (Figure 1). In both the post-eviction and transient phase, defecation rate decreased with increasing coalition size (Figure 1), while this relationship was positive during the settlement phase (Est = 1.53, SE = 0.54), both in the presence or absence of males (Figure 1). High rainfall during the previous month (Est = -0.59, SE = 0.35) and high maximum daily temperature (Est = -0.67, SE = 0.20) both decreased the rate of defecation.

Urination rate increased in the presence of males in the post-eviction phase (Est = 0.10, SE = 0.38), but males had a negative effect on urination during the transient (Est = -0.84, SE = 072) and settlement (Est = -1.20, SE = 0.59) phases (Figure 2; Table S2). In the presence of males, urination rate increased with increasing number of females throughout all phases (Est = 0.69, SE = 0.30), while this effect was not observed when males were absent (Figure 1). Rainfall and temperature did not affect the probability of urination (Table S2).

## DISCUSSION

Our study showed that defecation and urination rate of dispersing female meerkats varied among dispersal phases, with the presence of unrelated males, and with female coalition size. While we do not know what message, if any, is contained in faeces and urine, the observed

changes in defecation and urination patterns across different dispersal phases and social circumstances can be indicative of changes in scent marking-mediated communication purposes and patterns.

Defecation, but not urination, changed considerably across dispersal phases. The observed differences suggest that these two scent marking channels serve different purposes. This may be due to the different persistence of urine versus faeces in the dry climate and sandy substrate of the Kalahari Desert, where faeces are expected to be detectable for longer than urine (Monaghan et al. 1999). Accordingly, faeces may be used for long-term communication, while urine may serve as short-term information transfer. Long-term communication can be used for communication between far-apart groups or individuals, while short-term communication may be better suited for communication within groups or with individuals in the immediate vicinity (Allen et al. 2017). The observed increased defecation rate of dispersing meerkat females in the absence of males supports this hypothesis, for an increase in defecation is likely to increase the encounter probability with males through signalling the own presence. Our findings are in line with King et al. (2016) showing that ocelots increase the probability of defecation before pairing with unrelated mates. On the other hand, the observed increase in female urination in the presence of males is in line with the hypothesis that urination is used for intra-group communication. Short-lived urine scents may be used to reinforce and advertise the own social position and reproductive status to other coalition females and to the new males (Rajagopal et al. 2010). The use of urine (through over-markings) as a mean of within-group communication related to social and reproductive events has been shown for African wild dogs (*Lycaon pictus*) (Jordan et al. 2014). In the context of dispersal, attracting breeding partners and enhancing group formation and cohesion during the early stages of dispersal can reduce dispersal distance and facilitate settlement (Maag et al. 2018).

The overall low defecation rate during transience may result from the need to avoid detection from resident territorial groups, whose encounter could have severe physical

consequences (Christensen and Radford 2018). This is in line with recent findings, which showed that during transience dispersing meerkat coalitions avoid areas frequently used by unrelated resident groups (Cozzi et al. 2018). After settlement, however, coalitions need to advertise their presence to neighbouring groups to secure exclusivity over the new territory (Clobert et al. 2012), and they may do so by substantially increasing defecation rate. The use of faeces for territorial purposes has been recorded in other mammal species and was attributed to their long-lasting property compared to urine (Peters and Mech 1975).

Little is known about the use of chemical signals to mediate competition as compared to the use of physical aggression (Boydston et al. 2001; Jordan et al. 2010). The former having the advantage of minimizing potentially severe aggressive interactions with group members. In newly formed meerkat groups, competition to gain access to males conceivably increases with increasing number of females (Maag et al. *in review*). The observed positive association between urination rate and coalition size, in the presence of males, points towards the use of urine to mediate competition to gain access to breeding partners. Further research in this direction is, however, needed.

In the Kalahari Desert, rain and temperature are positively associated with water and food availability, which calls for an increase of elimination of metabolic wastes with increasing rainfall (Rimbach et al. 2018). Against our expectations, however, urination rate was not influenced by rainfall and temperature, and defecation was negatively affected by both variables. This unexpected result may be explained by the fact that the effect of nutrient availability on defecation and urination may be best reflected by the amount of faeces and urine eliminated at each excretion, which we did not measure, rather than by excretion rates. Excretion rates may thus reflect signalling needs, while the amount expelled may better reflect metabolic processes. The lack of a positive effect of rain on urination and defecation rates reinforces our belief that the observed patterns of defecation and urination rates were representative of scent mediated communication purposes, and they were not due to an increase

in food and water availability caused by higher rainfall. Our results on the effect of groups size and the presence of males on the deposition of faecal and urine scent marks can therefore be considered as conservative. Furthermore, it should be noted that we focused on defecation and urination rates during the active periods of the day; a change in these rates may also be caused by reallocation of the defecation or urination activity to inactive period of the day, such as in temporary sleeping burrows, in order to avoid conspecific aggression.

In conclusion, the observed variation in defecation and urination of female meerkats during dispersal and in relation to the social environment suggest that faeces and urine convey different types of signals. Increased female defecation prior to association with males and during the settlement process suggests that faeces are used for mate finding and territory defence, respectively. Both cases constitute extra-group communication, for which long-lasting faeces may be better suited, since sender and receiver are not present at the same time. On the other hand, urine may be used for short-term within-group communication purposes. This communication channel might simultaneously reduce aggressive interaction among group members and detection by potentially dangerous unrelated resident groups. We propose that urine can act as signal to advertise social and reproductive status to same-sex competitors and breeding partners. Our study thus shows how social factors influence scent marking during dispersal of a social mammal and gives insight to the function of scent marking in the formation of new groups. We advocate that future studies should incorporate scent marking when investigating important life-history events such as dispersal.

**ACKNOWLEDGEMENTS**

This study was financially supported by the Swiss National Science Foundation (Project CR32I3_159743). We thank the Northern Cape Conservation Authority for permission to conduct this research, and the farmers neighbouring the Kalahari Research Center for granting us access to their private land. We thank the field managers, volunteers, and field assistants for helping with data collection, in particular David Gaynor, Tim Vink, David Seager, Peter Clark,

Luc Le Grand, and Louis Bliard. We thank Tim Clutton-Brock and Marta Manser for providing access to research facilities and habituated study animals maintained by the Kalahari Meerkat Project, which has been supported by the European Research Council (Research Grant No 294494), the University of Zurich and the Mammal Research Institute at the University of Pretoria.

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## FIGURES

*Figure 1.* Effects of female meerkat coalition size and the presence of unrelated males on defecation probability, and how these effects differ among dispersal stages. Shown are model predictions with 95% confidence intervals.

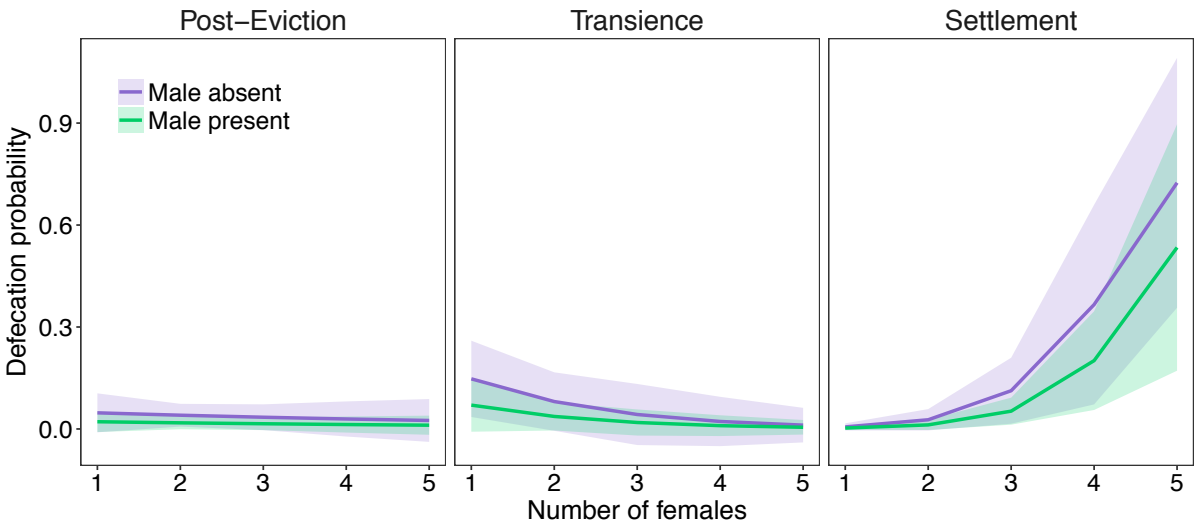
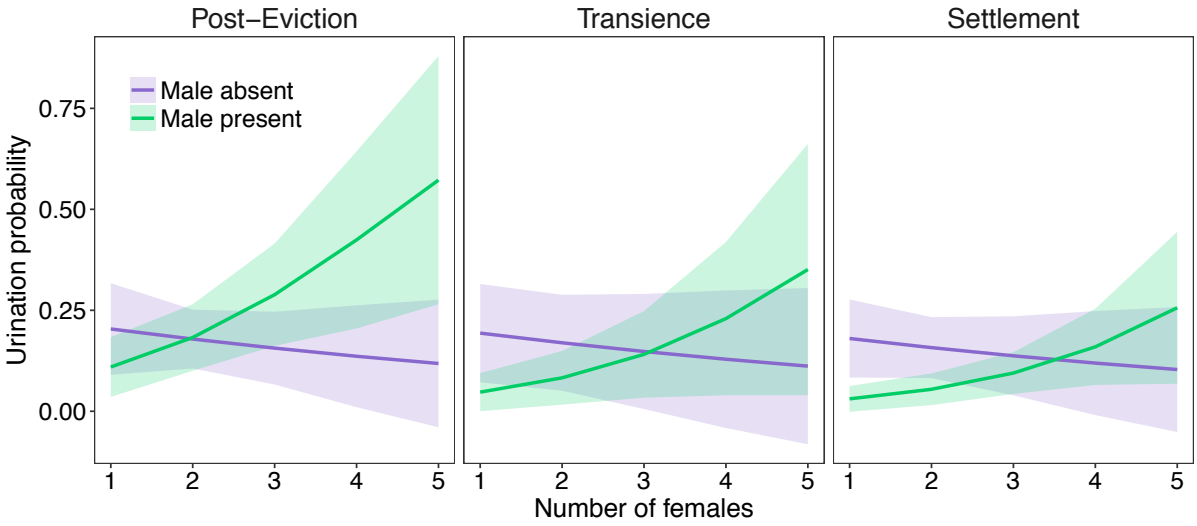


*Figure 2.* Effects of female meerkat coalition size and the presence of unrelated males on urination probability, and how these effects differ among dispersal stages. Shown are model predictions with 95% confidence intervals.



## SUPPLEMENTARY INFORMATION

**Table S1.** Upper table: all parameters included in the full model of the binomial GLMM investigating defecation probability (0 = no defecation; 1 = defecation). Middle table: results from model selection based on Akaike's information criterion (models from subset = delta<3 are shown); DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model based on AICc; W = Akaike weights. Lower table: details of best model; Estimate = model estimate; SE = standard error of model estimate; $R^2_m$ = marginal R squared; $R^2_c$ = conditional R squared.

| Response | Fixed | Variable description | Random |
|---|---|---|---|
| *def(0,1)* | *rain* | Rain sum of previous month | *ind ID* |
| | *temp* | Maximum daily temperature | *group ID* |
| | *stage* | Dispersal stage: Post-Eviction, Transience, Settlement | *year* |
| | *female* | Number of females in coalition | |
| | *male* | Male presence: Male present, Male absent | |
| | *stage:female* | | |
| | *stage:male* | | |
| | *female:male* | | |

| Variable | DF | AICc | ΔAICc |
|---|---|---|---|
| *male+temp+rain+female+stage+stage:female* | 12 | 218.51 | 0.00 |
| *temp+rain+female+stage+stage:female* | 11 | 219.23 | 0.72 |
| *male+temp+female+stage+stage:female* | 11 | 220.21 | 1.70 |
| *temp+female+stage+stage:female* | 10 | 220.44 | 1.93 |
| *male+temp+rain+female+stage+female:male+stage:female* | 13 | 220.61 | 2.10 |

| Variable | Estimate | SE | |
|---|---|---|---|
| *intercept* | -3.18 | 0.44 | $R^2_m$=0.20 |
| *rain* | -0.59 | 0.35 | $R^2_c$=0.23 |
| *temp* | -0.67 | 0.20 | |
| *stage(Transience)* | 0.68 | 0.66 | |
| *stage(Settlement)* | -0.25 | 0.67 | |
| *female* | -0.15 | 0.39 | |
| *male(present)* | -0.83 | 0.51 | |
| *stage(Transience):females* | -0.47 | 0.68 | |
| *stage(Settlement):females* | 1.53 | 0.54 | |

**Table S2.** Upper table: all parameters included in the full model of the binomial GLMM investigating urination probability (0 = no urination; 1 = urination). Middle table: results from model selection based on Akaike's information criterion (models from subset = delta<3 are shown); DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model based on AICc; W = Akaike weights. Lower table: details of best model; Estimate = model estimate; SE = standard error of model estimate; $R^2_m$ = marginal R squared; $R^2_c$ = conditional R squared.

| Response | Fixed | Variable description | Random |
|---|---|---|---|
| *uri(0,1)* | *rain* | Rain sum of previous month | *ind ID* |
| | *temp* | Maximum daily temperature | *group ID* |
| | *stage* | Dispersal stage: Post-Eviction, Transience, Settlement | *year* |
| | *female* | Number of females in coalition | |
| | *male* | Male presence: Male present, Male absent | |
| | *stage:female* | | |
| | *stage:male* | | |
| | *female:male* | | |

| Variable | DF | AICc | ΔAICc |
|---|---|---|---|
| *male+female+stage+female:male+stage:male* | 11 | 443.09 | 0.00 |
| *male+female+stage+female:male* | 9 | 443.25 | 0.16 |
| *male+temp+female+stage+female:male* | 10 | 443.61 | 0.52 |
| *male+temp+female+female:male* | 8 | 443.79 | 0.70 |
| *male+rain+female+stage+female:male+stage:male* | 12 | 444.13 | 1.04 |
| *male+temp+female+stage+female:male+stage:male* | 12 | 444.14 | 1.05 |
| *male+rain+female+stage+female:male* | 10 | 444.62 | 1.54 |
| *male+female+female:male* | 7 | 444.80 | 1.72 |
| *male+temp+rain+female+stage+female:male* | 11 | 445.03 | 1.94 |
| *temp* | 5 | 445.10 | 2.01 |
| *male+temp+rain+female+stage+female:male+stage:male* | 13 | 445.20 | 2.11 |
| *male+temp+rain+female+female:male* | 9 | 445.64 | 2.56 |
| *male+temp* | 6 | 445.70 | 2.61 |
| *male* | 5 | 445.76 | 2.67 |
| *stage* | 6 | 445.98 | 2.89 |

| Variable | Estimate | SE | |
|---|---|---|---|
| *intercept* | -1.54 | 0.25 | $R^2_m$=0.089 |
| *stage(Transience)* | -0.06 | 0.50 | $R^2_c$=0.094 |
| *stage(Settlement)* | -0.15 | 0.39 | |
| *female* | -0.15 | 0.22 | |
| *male(present)* | 0.10 | 0.38 | |
| *female:male(present)* | 0.69 | 0.30 | |
| *stage(Transience):male(present)* | -0.84 | 0.72 | |
| *stage(Settlement):male(present)* | -1.20 | 0.59 | |

# CHAPTER FIVE

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## Increased reproduction and decreased survival in dispersing helpers during group formation

To be submitted to *Ecology Letters*

Photo credit: Nino Maag

# Increased reproduction and decreased survival in dispersing helpers during new group formation

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**ABSTRACT**

Dynamics of socially and spatially structured populations are determined by within- and between-group dynamics, where the formation of new groups depends on the survival and reproduction of dispersing individuals. These demographic rates have, however, rarely been quantified in wild-living social species. We followed dispersing female meerkats (*Suricata suricatta*) for up to three years after new group formation and compared them to resident females. Dispersers had lower survival but higher conception rates than residents; and their conception and birth rates did not vary with social status, whereas subordinate reproduction was almost entirely suppressed by dominant females in resident groups. We propose that higher conception rates due to reduced reproductive suppression in the early stages of group formation allows for fast group augmentation. By showing persistent differences in demography between dispersers and residents, we highlight the need to investigate the entire, long-term dispersal process to assess regional dynamics of spatially structured populations.

**Keywords:** Delayed dispersal, long-distance dispersal, metapopulation, population dynamics, reproductive skew, cooperative species, spatially-explicit, vital rate

## INTRODUCTION

Through dispersal and group formation, subordinate helpers play a key role in the persistence of socially and spatially structured populations, as they can colonise locally extinct habitat patches (Hanski 1999). While helpers of social species can occasionally breed in their natal group, the majority of the group's reproduction is monopolised by a few breeding individuals (Koenig & Dickinson 2004). Therefore, subordinate helpers often disperse and form new groups to increase their own fitness through independent reproductive output (Keller & Reeve 1994). Measuring the survival and breeding success of dispersers in the wild has, however, proven challenging due to difficulties of following free-ranging individuals over long periods and distances (Tomkiewicz *et al.* 2010). These shortcomings often lead to assumptions that underestimate the survival and breeding of subordinate helpers, and consequently their contribution to average population fitness (Koenig *et al.* 1996; Cooper *et al.* 2008). To gain a comprehensive and spatially-explicit understanding of cooperative breeder dynamics, long-term life-history data of both dispersers and residents are needed (Belchion 1996).

A few studies have compared survival and breeding of dispersers to those of philopatric individuals across the entire dispersal event (Bonte *et al.* 2012; Waser *et al.* 2013). In cooperative species, however, information on demographic rates is limited mostly to the very early phases of dispersal (i.e., emigration) or to short-distance dispersal (Heg *et al.* 2004; Ridley *et al.* 2008; Armitage *et al.* 2011; Cram *et al.* 2018). Demographic information on long-distance dispersal is rare and anecdotal. However, the persistence of a socially and spatially structured population depends on the long-term success of long-distance dispersers to recolonise locally extinct, sometimes widely spread-out, territories and maintain gene flow (Ronce 2007). By systematically tagging and following dispersers for up to three years after emigration, we were able to robustly assess demographic rates through the different stages of dispersal and after settlement in a new territory for short- and long-distance dispersers and to compare them to those of resident individuals.

In many cooperative breeders, subordinate helpers disperse in multiple-member coalitions, as having more helpers at the initial stages of group formation increases reproductive success (Ligon & Ligon 1978; Packer & Pusey 1982; McNutt 1996; Lundy *et al.* 1998). The success of dispersal and colonization can therefore be expected to depend on the size of dispersal coalitions that experience faster group-size augmentation through increased cooperation (Brown *et al.* 1982; Clutton-Brock *et al.* 2001). In contrast, larger initial group size will lead to increased reproductive competition among individuals compared to smaller coalitions (Clutton-Brock 2002). However, because increase in group size is crucial during group formation, it can be expected that reproductive competition and skew in new groups is - at least initially - lower than in larger groups of origin (Kingma *et al.* 2014). As newly formed groups continue to increase in size, individuals will have to compete for long-term breeding opportunities again and reproductive skew may become more prominent. How reproduction in new groups is distributed among individuals and how it develops over time remains to be empirically tested.

Although individuals dispersing in large coalitions may alleviate some of the costs associated with dispersal (Packer *et al.* 1990; Bernasconi & Strassmann 1999; Wilson *et al.* 2002), dispersal remains a costly process and can have direct consequences on survival (Bonte *et al.* 2012). Each of the three stages of dispersal – emigration from the natal group, transience through unfamiliar landscape, and settlement in a suitable habitat – impose different costs on dispersing individuals (Bowler & Benton 2005). These are, for example, an increased predation and starvation risk during transience, or aggression from conspecifics and exposure to new pathogens after settlements (Bonte *et al.* 2012). In addition, unfamiliarity with the new habitat, which increases with dispersal distance, may have negative consequences such as reduced feeding efficiency (Pinter-Wollman *et al.* 2009). These can lead to patterns of condition loss and mortality varying among dispersal stages and with increasing dispersal distance (Bonte *et al.* 2012, Maag et al. *in review*).

In this study, we explored long-term survival and reproductive output of dispersing female meerkats (*Suricata suricatta*) and compared them to their resident counterparts. Meerkats are group-living, cooperative breeders and well suited to investigate demographic rates throughout the entire dispersal process. Resident meerkats live in groups of up to 50 individuals and are characterized by the presence of a dominant pair that monopolises reproduction and several related subordinate helpers (Griffin *et al.* 2003). The latter either remain in the natal group to raise their siblings or permanently disperse to form their own group (Maag *et al.* 2018). By delaying dispersal, subordinates benefit from increased cooperation (e.g., shared predator vigilance) in large natal groups. Due to reproductive competition, however, the dominant female often evicts one or multiple subordinate females who aggregate to same-sex multiple-member coalitions and disperse to become independent breeder (Clutton-Brock *et al.* 2008; Maag *et al.* 2018).

To investigate the demographic rates of dispersers in newly formed groups, we systematically followed the fate of both short- and long-distance dispersers that moved far beyond the main study area. For up to three years, we followed 63 dispersing female meerkats in 36 dispersing coalitions and compared them to 78 females in 13 resident groups. We visited females several times per week throughout the entire dispersal process and collect detailed data on the whole reproductive process including monthly conception and birth rates, litter size, weaning success, and recruitment (Fig. 1). We investigated survival and reproduction of dispersing and resident females of different social status and compared survival between the transient and settlement stages.

## METHODS

### *Data collection on dispersers*

Our study was conducted between September 2013 and March 2018 at the Kalahari Meerkat Project (KMP) located on the Kuruman River Reserve (26° 59’ S, 21° 50’ E), South

Africa. We fitted lightweight GPS radio collars (25 g, ~3.5 % of meerkat body mass) to subordinate females immediately after eviction from the natal, resident group. The collars were composed of a GPS module (CDD Ltd, Athens, Greece) and a VHF module (Holohil Systems Ltd, Ontario, Canada). To mount the collars, individuals were sedated using a mixture of isoflurane and oxygen in compliance with the KMP protocol (Jordan *et al.* 2007). All necessary permits to handle and tag meerkats were granted to the KMP by the Department of Environment and Nature Conservation of South Africa and the Animal Ethics Committee of the University of Pretoria (permit 'FAUNA 192/2014'). We used GPS locations to identify time of settlement and to calculate Euclidean dispersal distance from the natal group. We defined settlement based on visual investigation of the inflection point of the net squared displacement (NSD) plots (Cozzi *et al.* 2016). The NSD measures the square of the Euclidean distance from the place of eviction to any given GPS location along the dispersal path and is commonly used to investigate different dispersal modes and characterize the different stages of dispersal (Börger & Fryxell 2012)

We located dispersers by means of radio-tracking every two to seven days. At each visit, we collected the following data on female reproductive output: conception, birth, weaning, and pup survival to juvenile and recruit stages (Fig. 1). Conception was identified by abdominal swelling and associated weight increase (Sharp *et al.* 2013). Females give birth approximately 70 days after conception, which we assessed in the field by sudden weight loss and lactation marks (Sharp *et al.* 2013). One month after birth, pups are weaned and emerge from the burrow to forage with the group (Bateman *et al.* 2013). Pups reach nutritional independence two months after weaning, and are then described as juveniles (Bateman *et al.* 2013). Three months after nutritional independence, juveniles become subadults (Bateman *et al.* 2013), which corresponds to the age when we observed earliest dispersal. To get information on social status, at each visit we measured dominance-assertion behaviours as counts of aggressive interactions between individuals. In addition, we recorded data on age, temperature, rainfall, population

density, dispersing coalition size, and number of associated unrelated males, as these have been shown to affect dispersers (Maag *et al.* 2018).

*Data collection on residents*

We defined as resident any female born in an already-established group and older than six months at the time of a disperser's eviction. Females were considered as resident until they either dispersed or died. To consistently distinguish between dispersers and residents, founder females (i.e., females that started a group through dispersal in years prior to our study) were not considered as resident individuals. One individual per resident group carried a radio collar (Biotrack Ltd, Wareham, UK: 23 g) and groups were visited by volunteers several times each week as part of the long-term activities at the KMP (Clutton-Brock & Manser 2016). At each visit, volunteers recorded GPS locations with handheld GPS devices (Garmin Ltd., Kansas, USA). Volunteers also recorded information on female reproduction at the same level of detail as in dispersers. Information on social status, age, temperature, rainfall, population density, and group size were available from the KMP database (Bateman *et al.* 2013).

*Population density*

To estimate population density for each month (individuals/km$^2$), we divided the number of all resident individuals older than six months present in the study population by the size of the study area. We defined the size of the study area as the combination of 95 % kernel home ranges of all resident groups (Calenge 2006). These home ranges were either contiguous or partly overlapping. A detailed description of the methods and smoothing parameter estimators can be found in Cozzi et al. (2018).

*Climatic parameters*

Temperature and rainfall data were available from an on-site weather station. We used maximum daily temperature, which has been shown to reduce foraging time as meerkats avoid high midday temperatures by retreating into burrows or shaded areas (Doolan & Macdonald

1996a). We used the sum of daily rainfall in the previous month because rainfall in the past one month is an indicator of ecological conditions such as food availability (Hodge *et al.* 2009).

*Statistical modelling*

We tested for the effects of social status (i.e., dominant and subordinate), dispersing coalition size, and environmental factors on disperser and resident demographic rates. To ensure that covariates were not correlated with each other, we calculated variance inflation factors (Belsley *et al.* 2005) for coefficients in the full models. We standardised continuous variables across all data points used for a given model by subtracting their mean and then dividing by their standard deviation. Details for full models and model selections can be found in the Supporting Information (ST1-6). Model selection was based on Akaike's Information Criterion (AIC) and performed using the library *MuMin* (Bartoń 2018) in R (R Core Team 2013).

*1) Survival*

We used a Cox proportional hazard model with mixed effects implemented in the R library *coxme* (Therneau 2018) to investigate survival rates. We calculated the daily likelihood of death (i.e., hazard rate) $h[t]$ and used time-dependent covariates where each day $t$ appears as a separate observation. We right-censored individuals that were lost or still alive at the end of the study (63 out of 115 females) to account for their unknown fate beyond last detection (Fox & Weisberg 2011). To test for differences in survival between dispersers and residents (*strategy*) and between dominants and subordinates (*status*) we constructed a first Cox hazard model. To assess the variation in survival between dispersal stages (*stage*), and to investigate the influence of dispersal distance from the natal group (*dist*) on survival we compiled a second Cox hazard model with dispersers only.

In the first model, we included age (*age*), group size (coalition size for dispersers and group size for residents, *coal*), whether males were present or not (*male*), population density

(*pop*) and its quadratic effect (*pop*$^2$, Bateman *et al.* 2013), rainfall (*rain*), and temperature (*temp*) as further covariates. We also tested for two-way interactions between: female *strategy* and *status* to assess differences in reproductive skew between dispersers and residents (Clutton-Brock 1998); *strategy* and *age* to investigate if older individuals had an advantage during dispersal (Maag et al. *in review*), and *strategy* and *pop* to assess different effects of population density on dispersers and residents (Maag *et al.* 2018). In the second model, we only used the most important covariates from the first model because of lower sample size caused by the exclusion of residents: *coal*, *pop*, *pop*$^2$, *rain*, *temp*, and the interaction between *strategy* and *pop*. To control for repeated sampling across time and individuals, we used the random terms month of the year (*month*) and individual identity nested in natal group identity (*group/ind*) in both models. In addition, we compared the causes of mortality (i.e., predation, road kill, tuberculosis, injury) between residents and dispersers with separate binomial models.

*2) Conception and birth*

Dispersing females become pregnant at a certain rate and those that conceive can either give successful birth or abort the litter (Fig. 1). We used two generalised mixed effects models to investigate the monthly probabilities of conception and of birth as binomial response variables using the library *lme4* (Bates *et al.* 2014). We generated discrete-step censuses (as described in Paniw *et al. in review*) to obtain monthly conception (0 = no conception, 1= conception) and birth (0 = no birth, 1 = birth) probabilities for each individual. While conception probability was conditional on survival, birth probability was conditional on conception (Fig. 1). We used the same covariates as in the survival analysis: *strategy*, *status*, *age*, *coal*, *male*, *pop*, *pop*$^2$, *rain*, *temp*, and two-way interactions *strategy:status*, *strategy:age*, and *strategy*:*pop*. In addition, we tested whether time since eviction (*time*) had an influence on conception and birth rates in dispersers. We added a two-way interaction between *strategy* and *time* to assess if the cost associated with dispersal (e.g., elevated stress) affected conception and birth rates later in life; and a three-way interaction between *strategy*, *status*, and *time* to

investigate if these costs varied with social status (Creel *et al.* 2013, Maag *et al. in review*). For residents, we used the *time* elapsed since the day when group members were evicted, for comparison. In both models, we used the random terms month of the year (*month*) and individual identity nested in natal group identity (*group/ind*).

*3) Weaning, nutritional independence, and recruitment*

After a successful birth, many litters were lost during the weaning period, which lasts about a month (Fig. 1); we investigated the rate of successful weaning (≥1 pups emerged from the burrow) with a binomial mixed effects model. We then analysed the size of litters, conditional on successful weaning, by modelling the number of weaned pups (age = 1 month, Fig. 1), juveniles (3 months), and subadults (6 months) produced per successfully weaned litter using three generalised mixed effects models with Poisson distribution. We conducted all analyses using the library *lme4* and tested for, but found no evidence for, overdispersion in all three models (Ver Hoef & Boveng 2007). For the weaning analysis, we used the same covariates used for the conception and birth analysis, with one exception: we replaced *coal* (i.e., number of females and males) with number of females only (*#female*), because during this period the number of individuals that can lactate (i.e., allo-lactators) is likely to be more important than group size. For the independent juvenile and subadult recruit analyses we only used *strategy, status, age, coal, pop, rain and temp* due to reduced sample size (see ST4-6 for details). In all models, we used the random terms month of the year (*month*) and individual identity nested in natal group identity (*group/ind*).

**RESULTS**

Over the study period, we monitored 63 female meerkats in 36 dispersing coalitions forming 26 new groups (dispersers) and 78 females from 13 resident groups (residents). Females dispersed either alone or as several females at a time forming same-sex dispersing coalitions that ranged from 2 to 6 females and later grouped with none or up to 6 unrelated

males. Resident groups contained 1 to 12 females and 1 to 16 males. Overall, dispersing coalitions (and subsequent new groups) ranged from 2 to 9 individuals, and resident groups from 2 to 23 individuals. Dispersing females were between 6 months and 5.5 years of age at the time of eviction, and resident females were between 9 months and 8.8 years.

*1) Survival*

Dispersing females had significantly lower daily survival rates than their resident counterparts (Fig. 2a, Tab. 1), and predation rate was higher in dispersers than in residents (Fig. 2b, Est = -1.79, p = 0.031). In both dispersers and residents, survival rates did not differ significantly between dominant and subordinate females (Tab. 1). Population density had a positive effects on daily survival of dispersers and residents, and the presence of males had a positive effect on the survival of dispersers (Tab. 1). Neither dispersal distance nor dispersal stage affected dispersers' survival (ST1, Tab. S1b).

*2) Conception and birth*

There was a significant interaction effect between female strategy (i.e., disperser vs. resident) and social status (i.e., dominant vs. subordinate) on both conception and birth rates. In dispersers, conception and birth rates of subordinates were not different from those of dominants (Fig. 3a,b). In residents, however, subordinates conceived (Fig. 3a) and gave birth (Fig. 3b) less often than their dominant counterparts (Tab. 1). In the initial stages of group formation, dispersing females conceived more frequently then residents did during the same time (Fig. 3a, Tab. 1). This difference was mainly driven by the higher conception rate of subordinates in new groups compared to their resident counterparts. Over time, however, conception rate in dispersers decreased below that of residents, which remained constant (Fig. 3a). Resident dominants had the highest conception and birth rates of all four female strategies throughout the study period (Fig. 3a,b). Furthermore, conception rates of dispersers decreased with increasing population density, while those of residents stayed constant (Tab. 1, SF1). For

dispersers and residents alike, birth rates did not change over time or with increasing population density, but increased with increasing temperature and rainfall (Tab. 1). The presence of males had a positive effect on both conception and birth rates regardless of an individual being a disperser or a resident (Tab. 1).

*3) Weaning, nutritional independence, and recruitment*

There was no difference in weaning success between dispersers and residents (Tab. 1). Age of the mother and temperature positively influenced the likelihood of a litter being weaned, and the number of weaned pups per litter increased with the number of females in the group (Tab. 1). In dispersing coalitions, fewer pups per litter survived to the juvenile stage (nutritional independence at 3 months, Fig. 1) than in resident groups, and the number of juveniles per litter generally increased after periods with high rainfall (Fig. 3b, Tab. 1). The number of juveniles (6 months) per litter was not influenced by any of the model covariates for either dispersers or residents (ST6).

## DISCUSSION

The demographic rates of dispersers have rarely been followed throughout the entire dispersal process despite their predicted significance to influence the spatiotemporal dynamics of wildlife populations. In this study, we show that, despite a higher mortality and lower juvenile recruitment, dispersers of a cooperative species forming new groups, had markedly higher conception and birth rates compared to their resident counterparts. Furthermore, while conception and birth rates differed substantially between dominants and subordinates in established resident groups, our study shows that these rates were more equally distributed in dispersers. These increases in subordinate reproduction likely resulted from reduced reproductive suppression in newly formed groups, which potentially allow for fast augmentation. Here, we discuss the differences in survival and reproduction between dispersers

and residents and interpret these results with respect to their potential implications for group formation, habitat recolonisation, and regional population dynamics.

The observed increase in conception and birth rates of subordinate dispersers provides empirical support for the prediction that dispersers should have higher fitness than philopatrics to compensate for the high risks associated with dispersal (Keller & Reeve 1994; Kokko & Ekman 2002). Due to these high costs, subordinates of cooperative birds and mammals often delay dispersal and gain indirect fitness through raising close kin in the natal group (Hamilton & May 1977; Koenig & Dickinson 2004). To attain direct fitness in the natal group, females depend on rare extra-group matings with incoming males or have to wait in the queue for dominance to take over the breeding position (Young *et al.* 2007; Huchard *et al.* 2016). Our results show that dispersing females could increase their own reproductive rates even if they did not attain dominance in the new group. Furthermore, the route to inherit the dominance position is faster in new dispersal groups than at home because we show that survival of competitors is lower and dominance queues are typically shorter, which was recently shown in a cooperative bird species (Nelson-Flower *et al.* 2018). As such, the increased fitness prospects of dispersers can promote fast group augmentation and recolonisation success at the initial stages of group formation (Clutton-Brock 2002).

To increase group size faster, dominants in new groups may have made reproductive concessions to subordinates (Clutton-Brock 1998). The observed reduction of reproductive skew in new groups (i.e., subordinates attained similar reproduction to dominants) may then have led to higher overall conception rates in the initial stages of group formation in dispersers compared to residents (Keller & Reeve 1994). In addition, we expected that group augmentation is promoted by dispersal in large coalitions, as large initial group sizes may increase reproductive success (Brown *et al.* 1982). Our results provide empirical support for this expectation showing that large female coalitions had higher pup weaning success than small coalitions. However, a large initial group size may also increase the reproductive conflict

among females, potentially leading to a trade-off between large coalition size and reproductive competition (Clutton-Brock *et al.* 2008). As group size gradually increased with time after settlement, the point in time when conception rates of dispersers dropped below those of residents may indicate when the optimal balance exceeded. The optimal balance between the two factors may be crucial at the initial stage of group formation to recolonise extinct habitat patches and the key to regional population persistence.

Although we found differences between residents and dispersers in terms of reproductive output across social states, survival rates were not dependent on dominance status. This is in contrast to previous studies on cooperative breeders – including cooperative mammals and eusocial insects – showing that dominant individuals overall had higher survival than subordinate helpers (Bennett & Faulkes 2000; Keller & Jemielity 2006; Clutton-Brock *et al.* 2008). For example, recent work on meerkats has shown that dominant females overall – i.e., females that acquired dominance in their natal group and those that became dominant through dispersal and new group formation – have a longer lifespan than subordinates (Cram *et al.* 2018). This study, however, did not account for long-distance dispersal, but only considered newly formed dispersal groups within the study area. This could have led to an underestimation of subordinate survival because many dispersers were not considered in their survival estimates. Furthermore, the farthest dispersers are often the highest-quality individuals, which can be expected to have high survival (Hanski 1999; Stevens *et al.* 2014). The fact that dispersal distance did not affect dispersers' survival suggests that long-distance dispersers are indeed high-quality individuals and not considering them could have strong effects on survival estimates (Bowler & Benton 2009). In accordance with the absence of a distance effect, mortality during transience was not higher than during settlement. The difficulties of following dispersing helpers over long distances and the associated lack of information on high-quality dispersers likely lead to underestimation of subordinate survival and reproduction in many cooperative species (Koenig *et al.* 1996).

The observed lower survival and juvenile recruitment in dispersers compared to residents confirm that dispersal is costly, most likely due to unfamiliarity with the new area and reduced cooperation (Clutton-Brock *et al.* 2001; Pinter-Wollman *et al.* 2009; Bonte *et al.* 2012). The fact that dispersers experienced higher predation rates than residents further supports this interpretation. Our work thus extends previous findings on pre-dispersal prospecting behaviour in subordinates helpers of numerous species, which showed that being away from the group can be costly (Heg *et al.* 2004; Griesser *et al.* 2006; Ridley *et al.* 2008; Young & Monfort 2009). By assessing the fitness costs of dispersal throughout the entire dispersal process – including new group formation – our findings add to our understanding of delayed dispersal and philopatry in cooperative species (Koenig *et al.* 1992). However, we may have underestimated predation rate in residents because residents were visited more often and therefore more influenced by human presence than dispersers. In addition, cause of death could not always be identified for residents because individuals were not always recovered after disappearing from the group. Resident individuals could thus have disappeared either because they died or dispersed, which illustrates why mortality and dispersal rates are often difficult to distinguish (Cooper *et al.* 2008).

Although we do not show the population dynamic consequences of female dispersal here, our results on dispersal survival and reproductive output indicate the potential of female dispersing coalitions to be sources for extinct habitat patches. This is important because the meerkat system resembles a metapopulation with source-sink dynamics (Hanski 1999), where large resident groups may function as sources for large dispersal coalitions that can recolonise empty habitat patches. While dispersers from large source groups have previously been shown to augment smaller sink groups through immigration (Pusey & Packer 1987; Creel & Rabenold 1994; Bateman *et al.* 2013), information on new group formation is absent. In many cooperative species, however, female dispersers are not able to immigrate into existing groups, but must establish new breeding units (Wrangham 1980; Doolan & Macdonald 1996b; Clutton-

Brock & Lukas 2012). In those species, it is of special interest to investigate the contribution of female dispersers to regional dynamics, but has not been documented because dispersers are difficult to follow (Bowler & Benton 2005). This study is a first step towards a comprehensive understanding of dispersal and group formation in cooperative breeders.

We demonstrate that subordinate helpers who disperse and form new groups differ significantly in their demographic rates from resident individuals, with survival and reproductive skew being lower in new groups than in established resident groups. The detection of these dynamics relied on individual tagging of wild dispersing meerkats, their tracking through unfamiliar landscape over long distances, and the collection of high-resolution life-history data for extended periods after settlement. We suggest that it is important to account for long-distance dispersal and new-group formation when studying cooperative breeder population dynamics. This is because the dynamics of spatially and socially structured populations depend on both within- and between-group processes, with dispersal-related processes potentially having a large effect on these dynamics (Bowler & Benton 2005). By adding information on long-distance dispersal and new-group formation to existing knowledge on within-group processes, our study builds the foundation to assess the population-level consequences of dispersal.

**ACKNOWLEDGEMENTS**

This study was financially supported by the Swiss National Science Foundation (Project CR32I3_159743). We thank the Northern Cape Conservation Authority for permission to conduct this research, and the farmers neighbouring the Kalahari Research Center for granting us access to their private lands. We thank the field managers, volunteers, and field assistants for helping with data collection, in particular David Gaynor, Tim Vink, David Seager, Peter Clark, Luc Le Grand, Héctor Ruiz-Villar, Ana Morales-González, Louis Bliard, Natasha Harrison, and Frances Mullany. Our research relied on records of individual identities and life histories of meerkats, and research facilities maintained by the Kalahari Meerkat Project, which

has been supported by the European Research Council (Research Grant No 294494), the University of Zurich and the Mammal Research Institute at the University of Pretoria.

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## FIGURES AND TABLES

*Figure 1.* Stages of female reproduction and offspring development in meerkats. Each reproductive and developmental stage is conditional on making it to the previous stage. In grey are individuals that did not successfully carry through the current stage.

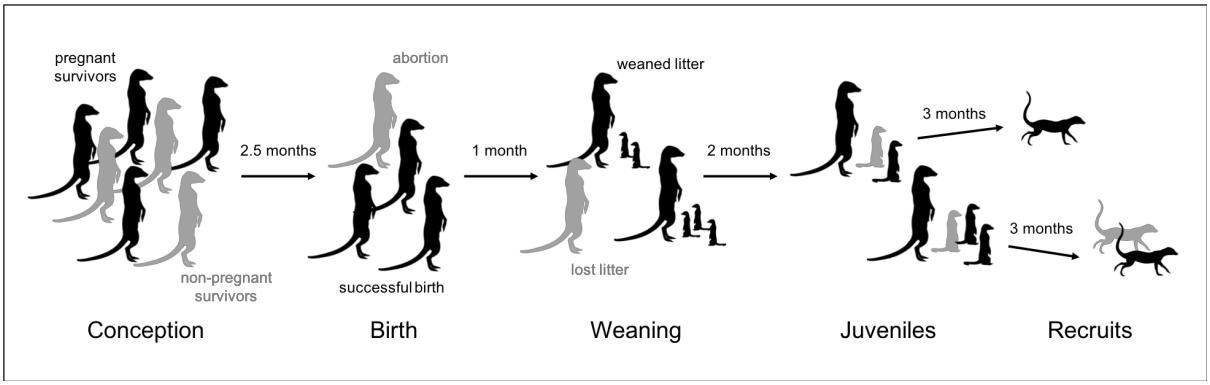

*Figure 2.* Difference in daily survival (a) and cause of death (b) between resident and dispersing female meerkats. a) Survival is depicted by model predictions and 95 % confidence intervals. b) Mortality was caused by predation, cars on roads, tuberculosis (TB), injuries, or unknown reasons.

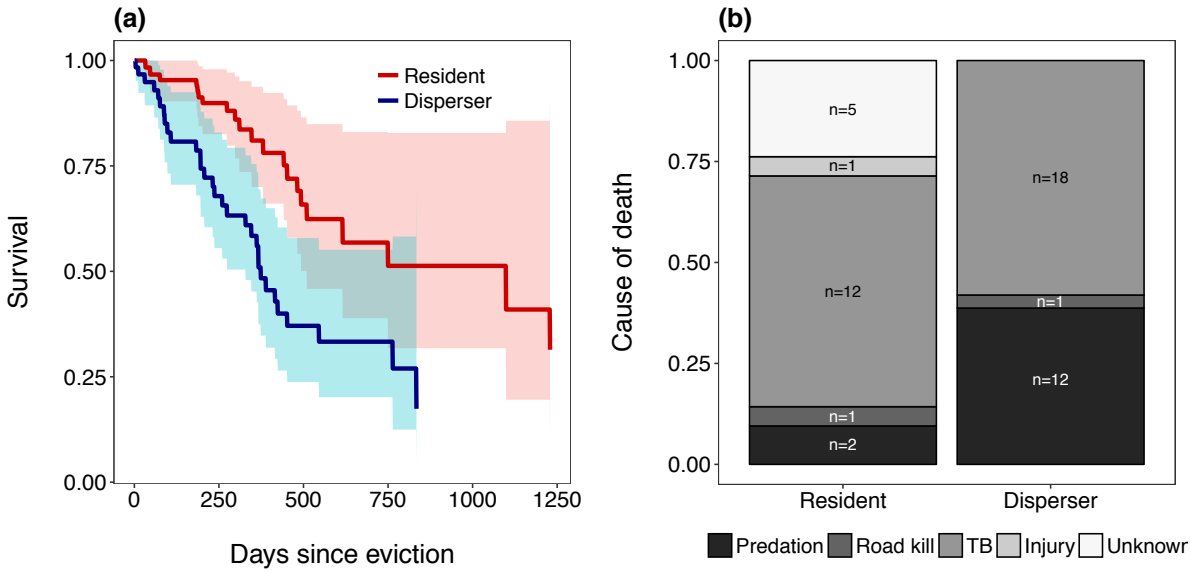

*Figure 3.* Difference in conception probability over time (a), birth probability (b), and number of produced juveniles (c) between resident and dispersing female meerkats depending on their social status. Shown are model predictions and 95 % confidence intervals.

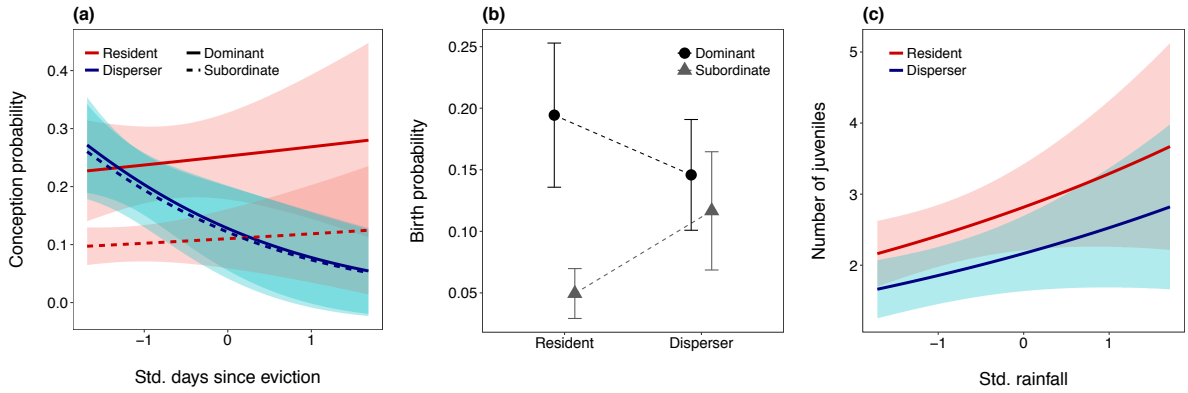

*Table 1.* Effects of individual, social, and environmental factors on survival and reproduction of female meerkats included in final models (top row). The estimate (Est) and standard error (SE) from the final model are reported for each term, as is the effect of removing each term from the final model on the model degrees of freedom (DF) and Akaike's Information Criterion for small sample sizes (ΔAICc). Significance (p) is based on Wald statistics. The explanatory variables are *strategy* = disperser vs. resident, *status* = dominant vs. subordinate, *male* = present vs. absent, *age* = female age, *pop* = population density, $pop^2$ = nonlinear effect of density, *time* = days since eviction, *#female* = number of females, *temp* = max daily temperature, *rain* = total rainfall of previous month.

| | Model | Est | SE | p | DF | ΔAICc |
|---|---|---|---|---|---|---|
| Survival | Cox hazard: *strategy+age+male+pop+strategy:age* | | | | 16 | 0 |
| | *- strategyDisp:age* | -0.54 | 0.40 | 0.180 | 15 | 0.66 |
| | *- malePresent* | 0.73 | 0.42 | 0.080 | 15 | 1.28 |
| | *- age (- strategy:age)* | -0.20 | 0.19 | 0.280 | 14 | 2.16 |
| | *- pop* | 0.85 | 0.21 | <0.001 | 12 | 11.84 |
| | *- strategyDisp (- strategy:age)* | -1.32 | 0.37 | <0.001 | 12 | 16.20 |
| Conception | Binomial: *strategy+status+male+pop$^2$+time+strategy:status+ strategy:time:+strategy:pop$^2$* | | | | 11 | 0 |
| | *- malePresent* | 0.60 | 0.32 | 0.063 | 10 | 1.67 |
| | *- time (- strategy:time)* | 0.03 | 0.10 | 0.726 | 9 | 1.79 |
| | *- strategyDisp:time* | -0.38 | 0.17 | 0.030 | 10 | 2.75 |
| | *- strategyDisp:statusDom* | -0.85 | 0.33 | 0.009 | 10 | 4.6 |
| | *- strategyDisp:pop$^2$* | -0.41 | 0.16 | 0.010 | 10 | 4.78 |
| | *- pop$^2$ (- strategy:pop$^2$)* | -0.08 | 0.13 | 0.515 | 9 | 8.99 |
| | *- statusDom (- strategy:status)* | 1.01 | 0.23 | <0.001 | 9 | 14.99 |
| | *- strategyDisp (- strategy:status, strategy:time, strategy:pop$^2$)* | 1.17 | 0.27 | <0.001 | 7 | 22.38 |
| Birth | Binomial: *strategy+dom+male+temp+rain+strategy:status* | | | | 9 | 0 |
| | *- temp* | 0.24 | 0.14 | 0.093 | 8 | 0.72 |
| | *- rain* | 0.26 | 0.12 | 0.036 | 8 | 2.15 |
| | *- malePresent* | 1.00 | 0.43 | 0.021 | 8 | 4.6 |
| | *- strategyDisp (- strategy:status)* | 0.97 | 0.29 | <0.001 | 7 | 7.95 |
| | *- strategyDisp:statusDom* | -1.19 | 0.37 | <0.001 | 8 | 8.39 |
| | *- statusDom (- strategy:status)* | 1.53 | 0.25 | <0.001 | 7 | 36.08 |
| Weaning | Binomial: *age+temp* | | | | 5 | 0 |
| | *- temp* | -0.36 | 0.18 | 0.046 | 4 | 1.85 |
| | *- age* | 0.61 | 0.22 | 0.005 | 4 | 5.59 |
| | Poisson: *#female* | | | | 4 | 0 |
| | *- #female* | 0.15 | 0.05 | 0.003 | 3 | 5.59 |
| Juvenile | Poisson: *strategy+rain* | | | | 5 | 0 |
| | *- strategyDisp* | -0.26 | 0.14 | 0.062 | 4 | 1.49 |
| | *- rain* | 0.14 | 0.06 | 0.027 | 4 | 2.17 |

## SUPPLEMENTARY INFORMATION

**Figure S1.** Difference in conception probability between resident and dispersing female meerkats depending on population density (individuals/km$^2$) and social status. Shown are model predictions and 95 % confidence intervals.

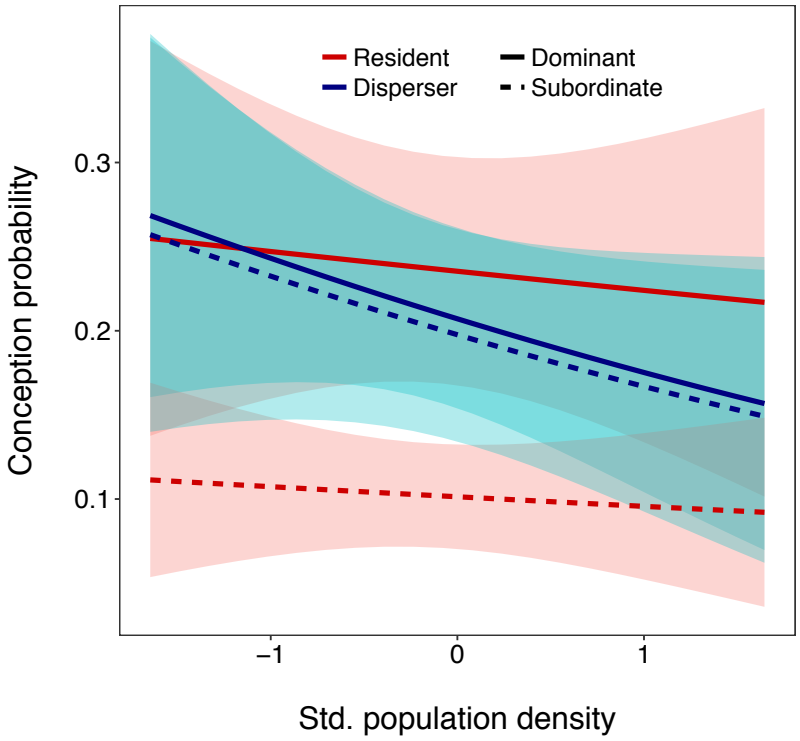

**Table S1a.** Cox proportional mixed effects model comparing survival of dispersers to that of residents. **Upper table:** Description of full statistical model. **Middle table:** Ten best models from model selection based on Akaike's information criterion; DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model. **Lower table:** Details of best model; Coef = coefficient; β = exponential coefficient; SE = standard error of Coef; Z = ratio of regression coefficient to standard error; p = significance; Chi = Chi-square score.

| Response | Explanatory | Description | Random |
|---|---|---|---|
| *surv(start,stop,death)* | *age* | Female age in months | *month* |
| | *strategy* | Factor: disperser vs resident | and |
| Females: n=115 | *status* | Factor: dominant vs subordinate | *group/ind* |
| Deaths: n=52 | *coal* | Number of individuals in coalition, group, respectively (including males) | |
| Days: n=38247 | *male* | Factor: male present vs absent | |
| | *pop* | Population density (individuals per $km^2$) | |
| | $pop^2$ | Nonlinear effect of population density | |
| | *rain* | Rain sum of the previous month | |
| | *temp* | Maximum daily temperature | |
| | *strategy:age* | | |
| | *strategy:status* | | |
| | $strategy:pop^2$ | | |

| Model | DF | AICc | ΔAICc |
|---|---|---|---|
| *strategy+male+age+pop+strategy:age* | 16 | 355.41 | 0 |
| *strategy+male+age+pop* | 15 | 356.07 | 0.66 |
| *strategy+age+pop+strategy:age* | 15 | 356.69 | 1.28 |
| $strategy+male+age+pop+strategy:age+strategy:pop^2$ | 17 | 357.01 | 1.6 |
| *strategy+male+age+pop+coal+strategy:age* | 17 | 357.02 | 1.62 |
| *strategy+male+age+pop+temp+strategy:age* | 17 | 357.09 | 1.68 |
| *status+strategy+male+age+pop+strategy:age* | 17 | 357.16 | 1.75 |
| *strategy+male+age+pop+rain+strategy:age* | 17 | 357.23 | 1.82 |
| *strategy+age+pop* | 14 | 357.32 | 1.91 |
| $strategy+male+age+pop+pop^2+strategy:age$ | 17 | 357.32 | 1.91 |

| Variable | Coef | β | SE | Z | p | |
|---|---|---|---|---|---|---|
| *strategyDisp* | 1.32 | 3.73 | 0.37 | -3.55 | <0.001 | Chi=43.41 |
| *age* | 0.20 | 1.22 | 0.19 | 1.07 | 0.280 | |
| *malePresent* | -0.73 | 0.48 | 0.42 | -1.75 | 0.080 | |
| *pop* | -0.85 | 0.43 | 0.21 | -4.04 | <0.001 | |
| *strategyDisp:age* | 0.54 | 1.72 | 0.40 | 1.35 | 0.180 | |

**Table S1b.** Cox proportional mixed effects model comparing survival between dispersal stages and depending on dispersal distance. **Upper table:** Description of full statistical model. **Middle table:** Ten best models from model selection based on Akaike's information criterion; DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model. **Lower table:** Details of best model; Coef = coefficient; β = exponential coefficient; SE = standard error of Coef; Z = ratio of regression coefficient to standard error; p = significance; Chi = Chi-square score.

| Response | Explanatory | Description | Random |
|---|---|---|---|
| surv(start,stop,death) | *stage* | Factor: transience vs settlement | *month* |
| | *dist* | Net displacement from place of eviction | and |
| Females: n=63 | *coal* | Number of individuals in coalition, group, respectively (including males) | *ind* |
| Deaths: n=31 | *pop* | Population density | |
| Days: n=15560 | $pop^2$ | Nonlinear effect of population density | |
| | *rain* | Rain sum of the previous month | |
| | *temp* | Maximum daily temperature | |
| | *strategy:pop* | | |
| | $strategy:pop^2$ | | |

| Model | DF | AICc | ΔAICc |
|---|---|---|---|
| $pop^2+pop+stage+stage:pop^2$ | 5 | 204.63 | 0 |
| $pop^2+stage$ | 5 | 204.69 | 0.06 |
| $pop^2+stage+stage:pop^2$ | 6 | 204.79 | 0.16 |
| $pop^2$ | 5 | 204.83 | 0.19 |
| $pop^2+pop+stage$ | 5 | 204.87 | 0.24 |
| $pop^2+pop$ | 5 | 205.3 | 0.67 |
| $pop^2+pop+stage+stage:pop^2+stage:pop$ | 5 | 205.3 | 0.67 |
| *pop+stage* | 5 | 205.54 | 0.91 |
| *stage* | 6 | 205.93 | 1.3 |
| $pop^2+dist$ | 6 | 206.13 | 1.5 |

| Variable | Coef | β | SE | Z | p | |
|---|---|---|---|---|---|---|
| *stageTrans* | 0.34 | 1.40 | 0.77 | 0.44 | 0.660 | Chi=10.37 |
| *pop* | -0.23 | 0.79 | 0.23 | -1.01 | 0.310 | |
| $pop^2$ | -0.37 | 0.69 | 0.25 | -1.50 | 0.130 | |
| $stageTrans:pop^2$ | 0.74 | 2.09 | 0.52 | 1.42 | 0.160 | |

**Table S2.** Binomial mixed effects model investigating conception rate. **Upper table:** Description of full statistical model. **Middle table:** Ten best models from model selection based on Akaike's information criterion; DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model. **Lower table:** Details of best model; Est = estimate; SE = standard error of Est; p = significance: $R^2_m$ = marginal R-squared, represents the variance explained by fixed effects; $R^2_c$ = conditional R-squared, represents the variance explained by both fixed and random effects.

| Response | Explanatory | Description | Random |
|---|---|---|---|
| *concept(0,1)* | *time* | Days since eviction | *month* |
| | *age* | Female age in months | and |
| Females: n=114 | *strategy* | Factor: disperser vs resident | *group/ind* |
| Pregnancies: n=242 | *status* | Factor: dominant vs subordinate | |
| Censuses: n=1257 | *coal* | Number of individuals in coalition, group, respectively (including males) | |
| | *male* | Factor: male present vs absent | |
| | *pop* | Population density (individuals per $km^2$) | |
| | *pop²* | Nonlinear effect of population density | |
| | *rain* | Rain sum of the previous month | |
| | *temp* | Maximum daily temperature | |
| | *strategy:time* | | |
| | *strategy:age* | | |
| | *strategy:status* | | |
| | *strategy:pop* | | |
| | *strategy:pop²* | | |
| | *strategy:status:time* | | |

| Model | DF | AICc | ΔAICc |
|---|---|---|---|
| *status+pop²+strategy+male+time+strategy:status+strategy:pop²+strategy:time* | 11 | 1172.3 | 0 |
| *status+pop²+strategy+male+coal+time+strategy:status+strategy:pop²+strategy:time* | 12 | 1173.44 | 1.14 |
| *status+pop²+strategy+male+age+time+strategy:status+strategy:pop²+strategy:time* | 12 | 1173.89 | 1.58 |
| *status+pop+pop²+strategy+male+time+strategy:status+strategy:pop²+strategy:time* | 12 | 1173.92 | 1.62 |
| *status+pop²+strategy+time+strategy:status+strategy:pop²+strategy:time* | 10 | 1173.97 | 1.67 |
| *status+pop²+strategy+male+strategy:status+strategy:pop²* | 9 | 1174.09 | 1.79 |
| *status+pop²+strategy+male+temp+time+strategy:status+strategy:pop²+strategy:time* | 12 | 1174.32 | 2.01 |
| *status+pop²+strategy+male+rain+time+strategy:status+strategy:pop²+strategy:time* | 12 | 1174.32 | 2.02 |
| *status+pop²+strategy+male+age+strategy:status+strategy:pop²* | 10 | 1174.4 | 2.09 |
| *status+pop²+strategy+strategy:status+strategy:pop²* | 8 | 1174.74 | 2.44 |

| Variable | Est | SE | p | |
|---|---|---|---|---|
| *intercept* | -2.66 | 0.38 | <0.001 | $R^2_m$=0.09 |
| *statusDom* | 1.01 | 0.23 | <0.001 | $R^2_c$=0.17 |
| *pop²* | -0.08 | 0.13 | 0.515 | |
| *strategyDisp* | 1.17 | 0.27 | <0.001 | |
| *malePresent* | 0.60 | 0.32 | 0.063 | |
| *time* | 0.03 | 0.10 | 0.726 | |
| *strategyDisp:statusDom* | -0.85 | 0.33 | 0.009 | |
| *strategyDisp:pop²* | -0.41 | 0.16 | 0.010 | |
| *strategyDisp:time* | -0.38 | 0.17 | 0.030 | |

**Table S3.** Binomial mixed effects model investigating birth rate. **Upper table:** Description of full statistical model. **Middle table:** Ten best models from model selection based on Akaike's information criterion; DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model. **Lower table:** Details of best model; Est = estimate; SE = standard error of Est; p = significance: $R^2_m$ = marginal R-squared, represents the variance explained by fixed effects; $R^2_c$ = conditional R-squared, represents the variance explained by both fixed and random effects.

| Response | Explanatory | Description | Random |
|---|---|---|---|
| *birth(0,1)* | *time* | Days since eviction | *month* |
| | *age* | Female age in months | and |
| Females: n=114 | *strategy* | Factor: disperser vs resident | *group/ind* |
| Pregnancies: n=168 | *status* | Factor: dominant vs subordinate | |
| Censuses: n=1253 | *coal* | Number of individuals in coalition, group, respectively (including males) | |
| | *male* | Factor: male present vs absent | |
| | *pop* | Population density (individuals per $km^2$) | |
| | *pop²* | Nonlinear effect of population density | |
| | *rain* | Rain sum of the previous month | |
| | *temp* | Maximum daily temperature | |
| | *strategy:time* | | |
| | *strategy:age* | | |
| | *strategy:status* | | |
| | *strategy:pop* | | |
| | *strategy:pop²* | | |
| | *strategy:status:time* | | |

| Model | DF | AICc | ΔAICc |
|---|---|---|---|
| *status+strategy+male+temp+rain+strategy:status* | 9 | 918.93 | 0 |
| *status+strategy+male+rain+strategy:status* | 8 | 919.65 | 0.72 |
| *status+strategy+male+temp+rain+coal+strategy:status* | 10 | 920.09 | 1.16 |
| *status+strategy+male+temp+rain+age+strategy:status* | 10 | 920.27 | 1.34 |
| *status+strategy+male+pop²+temp+rain+strategy:status* | 10 | 920.52 | 1.59 |
| *status+strategy+male+temp+rain+time+strategy:status* | 10 | 920.65 | 1.72 |
| *status+strategy+male+rain+coal+strategy:status* | 9 | 920.94 | 2.01 |
| *status+strategy+male+pop+temp+rain+strategy:status* | 10 | 920.96 | 2.03 |
| *status+strategy+male+rain+age+strategy:status* | 9 | 921.08 | 2.15 |
| *status+strategy+male+temp+strategy:status* | 8 | 921.08 | 2.15 |

| Variable | Est | SE | p | |
|---|---|---|---|---|
| *intercept* | -3.94 | 0.48 | <0.001 | $R^2_m$=0.13 |
| *statusDom* | 1.53 | 0.25 | <0.001 | $R^2_c$=0.24 |
| *strategyDisp* | 0.97 | 0.29 | 0.001 | |
| *malePresent* | 1.00 | 0.43 | 0.021 | |
| *temp* | 0.24 | 0.14 | 0.093 | |
| *rain* | 0.26 | 0.12 | 0.036 | |
| *strategyDisp:statusDom* | -1.19 | 0.37 | 0.001 | |

**Table S4a.** Binomial mixed effects model investigating litter weaning probability. **Upper table:** Description of full statistical model. **Middle table:** Ten best models from model selection based on Akaike's information criterion; DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model. **Lower table:** Details of best model; Est = estimate; SE = standard error of Est; p = significance: $R^2_m$ = marginal R-squared, represents the variance explained by fixed effects; $R^2_c$ = conditional R-squared, represents the variance explained by both fixed and random effects.

| Response | Explanatory | Description | Random |
|---|---|---|---|
| *wean(0,1)* | *time* | Days since eviction | *month* |
| | *age* | Female age in months | and |
| Females: n=73 | *strategy* | Factor: disperser vs resident | *group/ind* |
| Litters: n=168 | *status* | Factor: dominant vs subordinate | |
| | *#females* | Number of females in coalition, group, respectively | |
| | *male* | Factor: male present vs absent | |
| | *pop* | Population density (individuals per km$^2$) | |
| | *pop$^2$* | Nonlinear effect of population density | |
| | *rain* | Rain sum of the previous month | |
| | *temp* | Maximum daily temperature | |
| | *strategy:time* | | |
| | *strategy:status* | | |
| | *strategy:status:time* | | |

| Model | DF | AICc | ΔAICc |
|---|---|---|---|
| *age+temp* | 5 | 217.73 | 0 |
| *age+temp+#female* | 6 | 218.45 | 0.72 |
| *age+temp+status* | 6 | 218.89 | 1.16 |
| *age+temp+pop$^2$* | 6 | 218.92 | 1.19 |
| *age+temp+pop* | 6 | 219.45 | 1.72 |
| *age* | 4 | 219.57 | 1.85 |
| *age+temp+#female+pop$^2$* | 7 | 219.74 | 2.01 |
| *age+temp+time* | 6 | 219.78 | 2.05 |
| *age+temp+male* | 6 | 219.81 | 2.08 |
| *age+temp+rain* | 6 | 219.81 | 2.09 |

| Variable | Est | SE | p | |
|---|---|---|---|---|
| *intercept* | 0.54 | 0.19 | 0.005 | $R^2_m$=0.13 |
| *temp* | -0.36 | 0.18 | 0.046 | $R^2_c$=0.21 |
| *age* | 0.61 | 0.22 | 0.005 | |

**Table S4b.** Poisson mixed effects model investigating number of weaned pups. **Upper table:** Description of full statistical model. **Middle table:** Ten best models from model selection based on Akaike's information criterion; DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model. **Lower table:** Details of best model; Est = estimate; SE = standard error of Est; p = significance: $R^2_m$ = marginal R-squared, represents the variance explained by fixed effects; $R^2_c$ = conditional R-squared, represents the variance explained by both fixed and random effects.

| Response | Explanatory | Description | Random |
|---|---|---|---|
| *#pup* | *time* | Days since eviction | *month* |
| | *age* | Female age in months | and |
| Females: n=51 | *strategy* | Factor: disperser vs resident | *group/ind* |
| Litters: n=102 | *status* | Factor: dominant vs subordinate | |
| | *#females* | Number of females in coalition, group, respectively | |
| | *male* | Factor: male present vs absent | |
| | *pop* | Population density (individuals per $km^2$) | |
| | *pop²* | Nonlinear effect of population density | |
| | *rain* | Rain sum of the previous month | |
| | *temp* | Maximum daily temperature | |
| | *strategy:time* | | |
| | *strategy:status* | | |
| | *strategy:status:time* | | |

| Model | DF | AICc | ΔAICc |
|---|---|---|---|
| *#female* | 4 | 390.3 | 0 |
| *#female+strategy* | 5 | 390.87 | 0.57 |
| *#female+pop* | 5 | 391.13 | 0.83 |
| *#female+rain* | 5 | 391.6 | 1.3 |
| *#female+strategy+pop* | 6 | 391.84 | 1.53 |
| *#female+male* | 5 | 391.84 | 1.53 |
| *#female+strategy+rain* | 6 | 392.06 | 1.75 |
| *#female+age* | 5 | 392.28 | 1.97 |
| *#female+temp* | 5 | 392.33 | 2.02 |
| *#female+status* | 5 | 392.42 | 2.12 |

| Variable | Est | SE | p | |
|---|---|---|---|---|
| *intercept* | 1.27 | 0.06 | <0.001 | $R^2_m$=0.08 |
| *#female* | 0.15 | 0.05 | 0.003 | $R^2_c$=0.12 |

**Table S5.** Poisson mixed effects model investigating number of produced juveniles. **Upper table:** Description of full statistical model. **Middle table:** Ten best models from model selection based on Akaike's information criterion; DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model. **Lower table:** Details of best model; Est = estimate; SE = standard error of Est; p = significance: $R^2_m$ = marginal R-squared, represents the variance explained by fixed effects; $R^2_c$ = conditional R-squared, represents the variance explained by both fixed and random effects.

| Response | Explanatory | Description | Random |
|---|---|---|---|
| *#pup* | *age* | Female age in months | *month* |
| | *strategy* | Factor: disperser vs resident | and |
| Females: n=51 | *status* | Factor: dominant vs subordinate | *group/ind* |
| Litters: n=102 | *coal* | Number of individuals in coalition, group, respectively (including males) | |
| | *pop* | Population density (individuals per $km^2$) | |
| | *rain* | Rain sum of the previous month | |
| | *temp* | Maximum daily temperature | |
| | *strategy:status* | | |

| Model | DF | AICc | ΔAICc |
|---|---|---|---|
| *rain+strategy+age* | 5 | 378.33 | 0 |
| *rain+age* | 5 | 378.36 | 0.03 |
| *rain+strategy+age* | 6 | 378.47 | 0.14 |
| *rain* | 4 | 379.63 | 1.3 |
| *rain+pop+age* | 6 | 379.82 | 1.49 |
| *rain+status+strategy* | 6 | 379.84 | 1.5 |
| *rain+age+coal* | 6 | 380.04 | 1.71 |
| *rain+strategy+pop* | 6 | 380.18 | 1.85 |
| *rain+strategy+pop+age* | 7 | 380.19 | 1.86 |
| *strategy* | 4 | 380.5 | 2.17 |

| Variable | Est | SE | p | |
|---|---|---|---|---|
| *intercept* | 0.88 | 0.09 | <0.001 | $R^2_m$=0.08 |
| *strategyDisp* | -0.26 | 0.14 | 0.062 | $R^2_c$=0.09 |
| *rain* | 0.14 | 0.06 | 0.027 | |

**Table S6.** Poisson mixed effects model investigating number of produced subadults. **Upper table:** Description of full statistical model. **Middle table:** Ten best models from model selection based on Akaike's information criterion; DF = degrees of freedom; AICc = AIC for small sample sizes; ΔAICc = difference to best statistical model.

| Response | Explanatory | Description | Random |
|---|---|---|---|
| *#pup* | *age* | Female age in months | *month* |
| | *strategy* | Factor: disperser vs resident | and |
| Females: n=40 | *status* | Factor: dominant vs subordinate | *group/ind* |
| Litters: n=79 | *coal* | Number of individuals in coalition, group, respectively (including males) | |
| | *pop* | Population density (individuals per $km^2$) | |
| | *rain* | Rain sum of the previous month | |
| | *temp* | Maximum daily temperature | |
| | *strategy:status* | | |

| Model | DF | AICc | ΔAICc |
|---|---|---|---|
| ***Null*** | 3 | 283.96 | 0 |
| *rain* | 4 | 284.16 | 0.2 |
| *temp* | 4 | 285.15 | 1.2 |
| *rain+temp* | 5 | 285.5 | 1.54 |
| *age* | 4 | 285.54 | 1.58 |
| *pop* | 4 | 285.59 | 1.63 |
| *rain+pop* | 5 | 285.84 | 1.89 |
| *strategy* | 4 | 285.9 | 1.94 |
| *rain+age* | 5 | 286.05 | 2.09 |
| *rain+strategy* | 5 | 286.07 | 2.12 |

# CHAPTER SIX

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## Prolonged gestation as response to social suppression and hostile environment: an adaptive strategy in dispersing meerkats

To be submitted to *Nature*

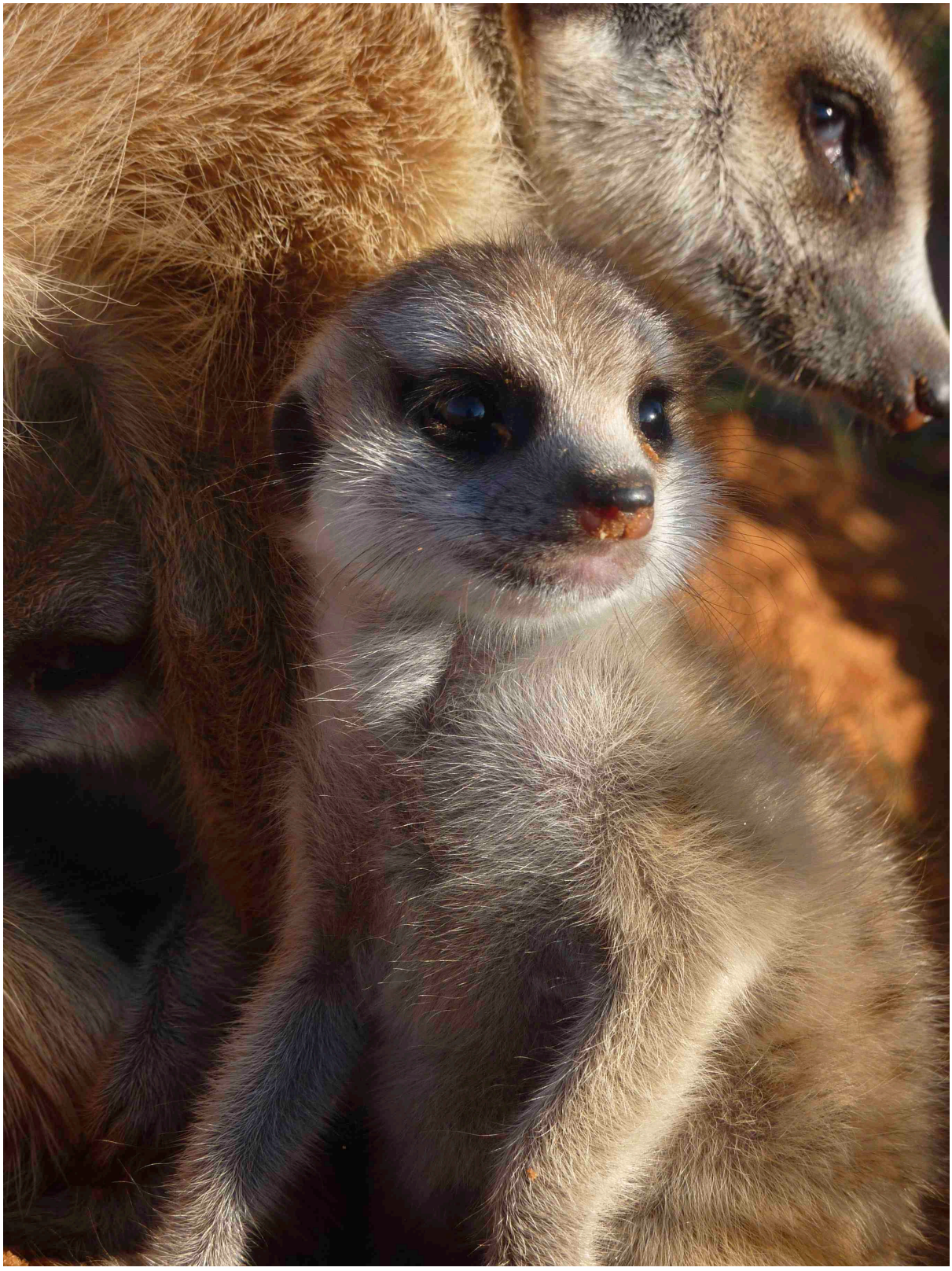

Photo credit: Nino Maag

# Prolonged gestation as response to social suppression and hostile environment: an adaptive strategy in dispersing meerkats

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**SUMMARY**

Lactation is the most energetically demanding period of the mammalian reproductive cycle [1,2] and parturition should therefore coincide with periods of optimal productivity to assure offspring growth and survival [3]. To time parturition with favourable conditions, mammals can adjust gestation length by either delaying implantation of the blastocyst or by suspending post-implantation embryonic development (i.e., delayed development) [4]. The latter decouples implantation from parturition and gives an individual more flexibility in adjusting parturition timing. While delayed implantation is common in mammals [5–7], delayed development is very rare and has only been observed in a few bat species [8,9]. Here we show that pregnant dispersing meerkats (*Suricata suricatta*), which are forced out of their natal territory due to reproductive suppression and experience extended periods of unfavourable conditions, prolong their gestation by means of delayed development. We performed repeated ultrasound scans on wild, unanesthetized females throughout their pregnancies and found that dispersers prolonged their post-implantation period at an average of 20 % compared to residents. The longest post-implantation period was 64 days in dispersers and the shortest was 35 days in residents. Our results suggest that pregnant dispersers delay parturition until they find suitable habitat to form a new group and raise a first successful litter. Delayed development is likely to be especially beneficial for social species that live in harsh environments and use social cues for the optimal timing of birth.

**MAIN TEXT**

Although gestation length in mammals is very consistent within species [10], various mechanisms have evolved to delay parturition [4]. Delayed implantation occurs in nine mammalian orders and describes the temporary suspension of the blastocyst and its attachment to the uterus [4]. It allows mating when both male and female are in peak physical condition and has been shown to be dependent on maternal [6], environmental [11,12], and social [7] factors. The fact that delayed implantation has been observed in a wide range of species shows its ecological significance and suggests that it has evolved independently several times [13]. On the contrary, delayed embryonic development after implantation in the uterus is very rare and has only been observed in ten bat species [4]. It describes the suspension or arrest of post-implantation embryogenesis [4] and has been shown to be temperature induced [8,14]. Although embryonic staging and suspension are understood in bats [15,16], little is known about physical and social environmental influences on delayed development. It has been suggested that delayed development is stress induced, and the ability to delay development could therefore be adaptive in situations where habitat quality is low and competition high [17].

As delayed embryonic development provides increased plasticity to the extent over which an embryo is in the reproductive tract, it may be especially beneficial for species that experience stress due to immediate social and environmental cues. In subordinates of social breeders, who are subjected to stress-induced reproductive suppression [18], variability in post-implantation development time could facilitate abortion or prolongation of gestation depending on the current social situation [4,19]. Often pregnant subordinates are forced to disperse due to reproductive competition and the additional costs associated with dispersal will further increase stress levels (Maag et al. *in review*). Hence, abortion before dispersal or prolongation of gestation until available habitat is found could represent a highly adaptive strategy. Here, we show that wild dispersing meerkats delay parturition, and we suggest delayed embryonic

development as the mechanism thereof. To our knowledge, this is the first observation of delayed embryonic development in a member of the carnivore order.

Meerkats are cooperative breeders that live in groups of 2-50 individuals, which are characterized by a dominant pair that monopolises reproduction and several closely related subordinate helpers [20]. The dominant female aggressively evicts subordinates when they are pregnant, and evicted females either abort their pregnancy and return to their group or permanently disperse [19,21]. To attain independent breeding, subordinate females have to disperse, and the high costs of dispersal can be expected to induce strong selective pressure on their reproduction [22] . Pregnancy in female meerkats lasts 70 days and abdominal growth and weight increase start 28 days after conception [23]. The ability to delay parturition until a new suitable territory is found might be essential for survival of the first litter, group augmentation, and successful colonisation [24] (Maag et al. *in prep*). We used a combination of visual pregnancy assessment, frequent weight measurements, and ultrasound monitoring to investigate variability in post-implantation development duration in dispersing meerkats and compared them to resident females.

We measured the length of 96 pregnancies in 46 dispersers and 258 pregnancies in 103 residents. We detected pregnancies due to a swelling of the abdomen and associated weight gain, which approximately coincides with implantation (hereafter referred to as "pregnancy assessment", Fig. 1). We identified parturition from a sudden change in abdominal shape and weight loss [23]. As individuals were trained to climb onto a portable weighing scale allowing for regular weight measures, we could determine meerkat pregnancies with high certainty. However, pregnancies are notoriously difficult to observe in wild animals and – in addition – competition for breeding positions can lead to a secondary growth spur in individuals of social species [25]. As dispersal and new group formation are likely to coincide with dominance competition (Maag et al. *in review*), competitive growth spurs could lead to misdating of pregnancy assessment. Hence, to obtain accurate measurements of post-implantation

development duration, we monitored the pregnancies of five dispersers and five residents with a portable ultrasound machine in the field (Model S6BW, SonoScape Ltd, Nanshan, China, Fig. 2, Extended Data Tab. 1). Ultrasound scans were executed every 4-7 days without anaesthesia, and we obtained image time series of embryonic development from immediately after implantation until parturition (Fig. 3, Extended Data Tab. 2). We only used ultrasound scans of pregnancies that produced live offspring.

Both methods – i.e., visual pregnancy assessment supported by weight trajectories and ultrasound monitoring – showed that, on average, dispersing females had longer pregnancies than resident females (Fig. 4). In the visual assessment, dispersers had an average post-implantation development time of 45 ± 1.6 days while that of residents was 39 ± 0.7 days (LMM: Est = 0.20, $p < 0.001$, see methods). The ultrasound scans revealed that dispersers can indeed prolong their pregnancies by means of delayed development, with an average post-implantation duration of 57 ± 1.4 days in dispersers and 47 ± 4.2 days in residents (LM: Est = 9.31, $p = 0.036$). This means that dispersers prolonged their post-implantation time at an average of 20 %. Post-implantation development times ranged from 35 days in resident to 64 days in dispersers (Extended Data Tab. 1). In humans, this would correspond to a variation in post-implantation gestation length between 179 and 327 days (i.e., less than 6 months to almost 11 months), considering an average post-implantation period of 271 days. Hence, post-implantation development time in meerkats can vary by up to 80 %, which provides exceptional flexibility to time parturition according to immediate changes in the physical and social environment.

The ultrasound images confirm that the observed delay is not due to delayed implantation, since the amniotic sac – and in some cases the epiblast – are clearly visible on the early scans (Fig. 3, SI Video & Image files), showing that the embryo has transitioned from implantation stage to gastrulation [9,16,17]. We further present an anecdotal finding showing that the rate of embryonic development after the first scan can be very different among females:

Two sisters that implanted at the same time and resided in the same group showed very different embryo development trajectories after the epiblast was already visible (see VPAF037 and VPA038 in Extended Data Tab. 2). We scanned both females on the same days and while embryo sizes were very similar during the first scan (0.4-0.6 $cm^2$ = 2-3 days after implantation), embryo size increased twice as fast in VPAF038 as in VPAF037 on the later scans (SI Video files). This late delay of embryogenesis is most curious as it has been suggested that the metabolic demands associated with delayed embryonic development are lower if delays occur early during gestation compared to later delays during development [4]. The costs of maintaining an embryo for extended periods may be the reason for delayed development to occur less often than other delays such as delayed fertilisation or delayed implantation.

The extent to which meerkats can prolong their post-implantation development (max. 80 %) is similar to those of the Jamaican fruit bat (*Artibeus jamaicensis*, 65 %) [9] and short-tailed fruit bat (*Carollia perspicillata*, 60%) [17], but shorter than those of the California leaf-nosed bat (*Macrotus californicus*, 100 %) [8] and Philippine pygmy fruit bat (*Haplonycteris fischeri*, 200 %) [26]. In all these bat species, embryonic development was delayed immediately after implantation when the blastocyst had divided into outer trophoderm and inner embryonic cell mass, and had reached the primitive streak stadium at the start of gastrulation [8,9,17,26]. These studies used histological tissue samples because embryos are not yet visible on ultrasound during these early stages. This means that delay in meerkats occurs much later during embryonic development than in bats, which is exceptional and could provide a female with even more flexibility to respond to immediate changes in the environment and social circumstances. However, an animal may be limited in the extent to which it can delay the later stages of development, potentially explaining the shorter delays in meerkats compared to many bats.

Our findings suggest that subordinate meerkats can adjust their pregnancy length in response to reproductive suppression and eviction from the natal group. Increased social stress

during eviction [18] and later during dispersal (Maag et al. *in review*) may have led to a temporary arrest or decreased rate of embryonic development [17]. Therefore, the initiation of this stress response – and hence the variation in pregnancy length – seems to be a question of sociality. Adaptation of pregnancy length to reproductive conflict may be a common trait in social mongooses, as subordinates of the cooperatively breeding banded mongoose (*Mungo mungo*) give birth earlier and synchronise parturition with the dominant female to avoid infanticide [30]. This is interesting as in most other animals, gestational delays depend on abiotic factor such as food availability, temperature, or spring conditions [11,12]. Stressors such as unfamiliar landscape and increased predation pressure during dispersal could have added to the costs of social stressors. A stress-related mechanism to prolong pregnancies in dispersers may be adaptive, as giving birth after settlement is likely to increase their fitness [3]. This may be especially important in dispersers of cooperative breeders that depend on a first successful litter to augment a newly established group [24] (Maag et al. *in prep*).

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**Acknowledgements.** This study was financially supported by the Swiss National Science Foundation (Project CR32I3_159743). We thank the Northern Cape Conservation Authority for permission to conduct this research, and the farmers neighbouring the Kalahari Research Center for granting us access to their private lands. We thank the field managers, volunteers, and field assistants for helping with data collection, in particular David Gaynor, Tim Vink, David Seager, Peter Clark, Luc Le Grand, Héctor Ruiz-Villar, Ana Morales-González, Louis Bliard, Natasha Harrison, and Frances Mullany. We thank Stuart Patterson for consultation on pregnancy assessment, Glauco Camenisch for maternity analysis, and Constance Dubuc for discussions on hormonal aspects of the reproductive cycle. We thank Marta Manser for providing access to research facilities and habituated study animals maintained by the Kalahari Meerkat Project, which has been supported by the European Research Council (Research Grant No 294494), the University of Zurich, and the Mammal Research Institute at the University of Pretoria.

**Author Contributions.** NM, GC, DS, and AO conceived the idea for the study. NM and DS collected data on dispersing individuals and performed ultrasound. NM performed statistical modelling and wrote the manuscript. TCB led the collection of data on resident groups. All authors substantially contributed to the final draft.

**Author Information.** The authors declare no competing interests. All correspondence and material requests should be addressed to N. Maag at nino.maag@gmail.com.

## FIGURES

**Figure 1 | Weight trajectories of pregnant meerkats.** Examples of weight increase in a dispersing and a resident meerkat from the same natal group (i.e., daughter and mother, respectively) that conceived approximately on the same date. Note that the initial weight increase in the disperser could have been due to her transition to dominance and we thus additionally used ultrasound to proof prolonged pregnancies. Pregnancy assessment refers to the time when first abdominal swelling was observed and approximately coincides with implantation date.

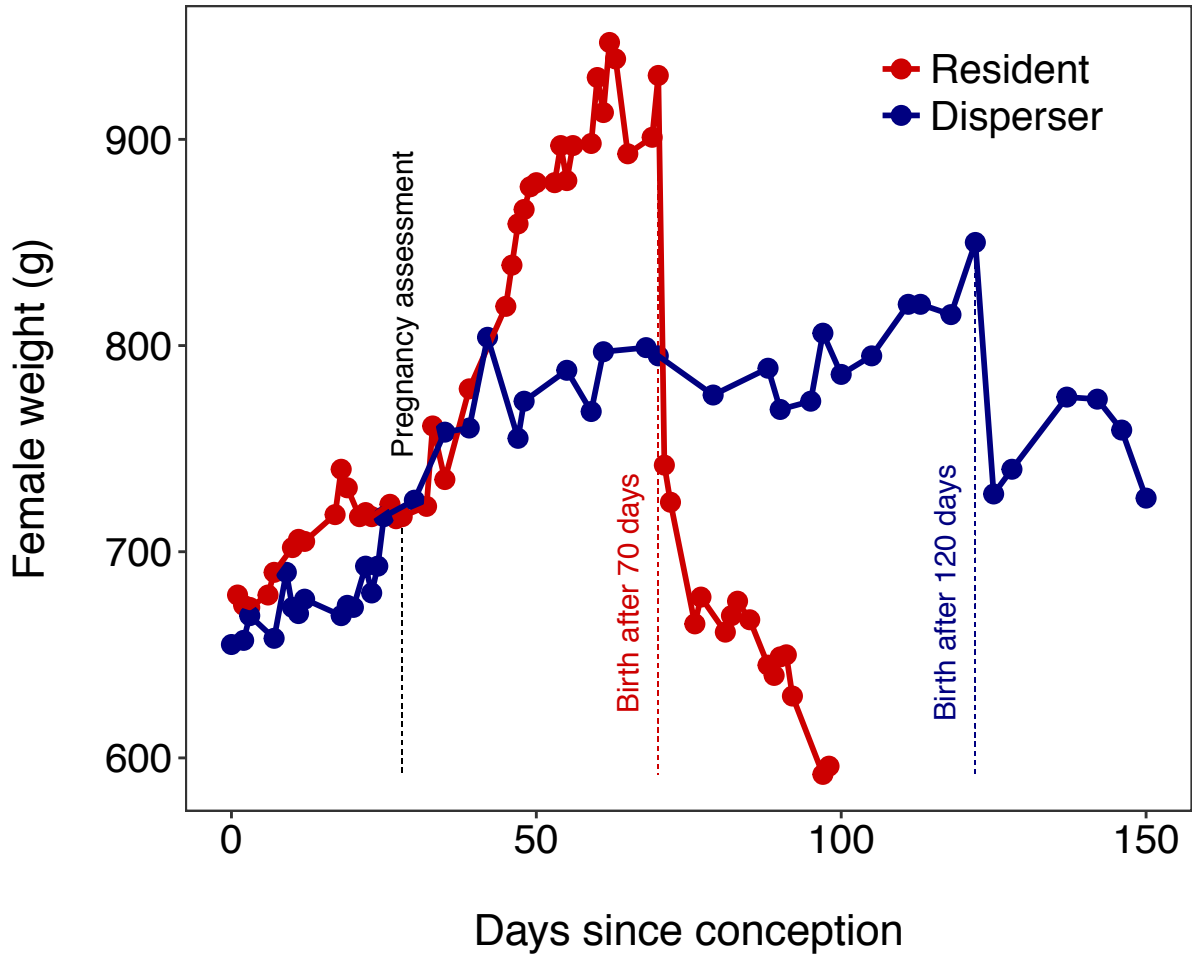


**Figure 2 | Ultrasound scanning of wild meerkats in the field.** We conducted ultrasound scans on unanesthetized meerkats with a portable ultrasound machine. Animals were trained to hold still and be scanned with the ultrasound probe by providing small amounts of water and egg.

**Figure 3 | Cross-sectional ultrasound scans of embryos during developmental stages of a meerkat gestation.** Embryonic development 1 day (**a**), 10 days (**b**), 30 days (**c**), and 50 days (**d**) after implantation in the uterus. 1 = fluid-filled amniotic sac, 2 = maternal spine, 3 = fetus, 4 = fetal heart, 5 = fetal spine. **a**, The embryo soon after implantation, the inner cell mass of the blastocyst has already divided into amniotic sac and epiblast. **b**, The fetal tissue is clearly visible inside the amniotic cavity. **c**, Features such as head and pelvis of fetuses are visible. **d**, One day before parturition the fetus is larger than the probe section and only one fetus is visible. The scales along the right picture margins are given in centimetre.

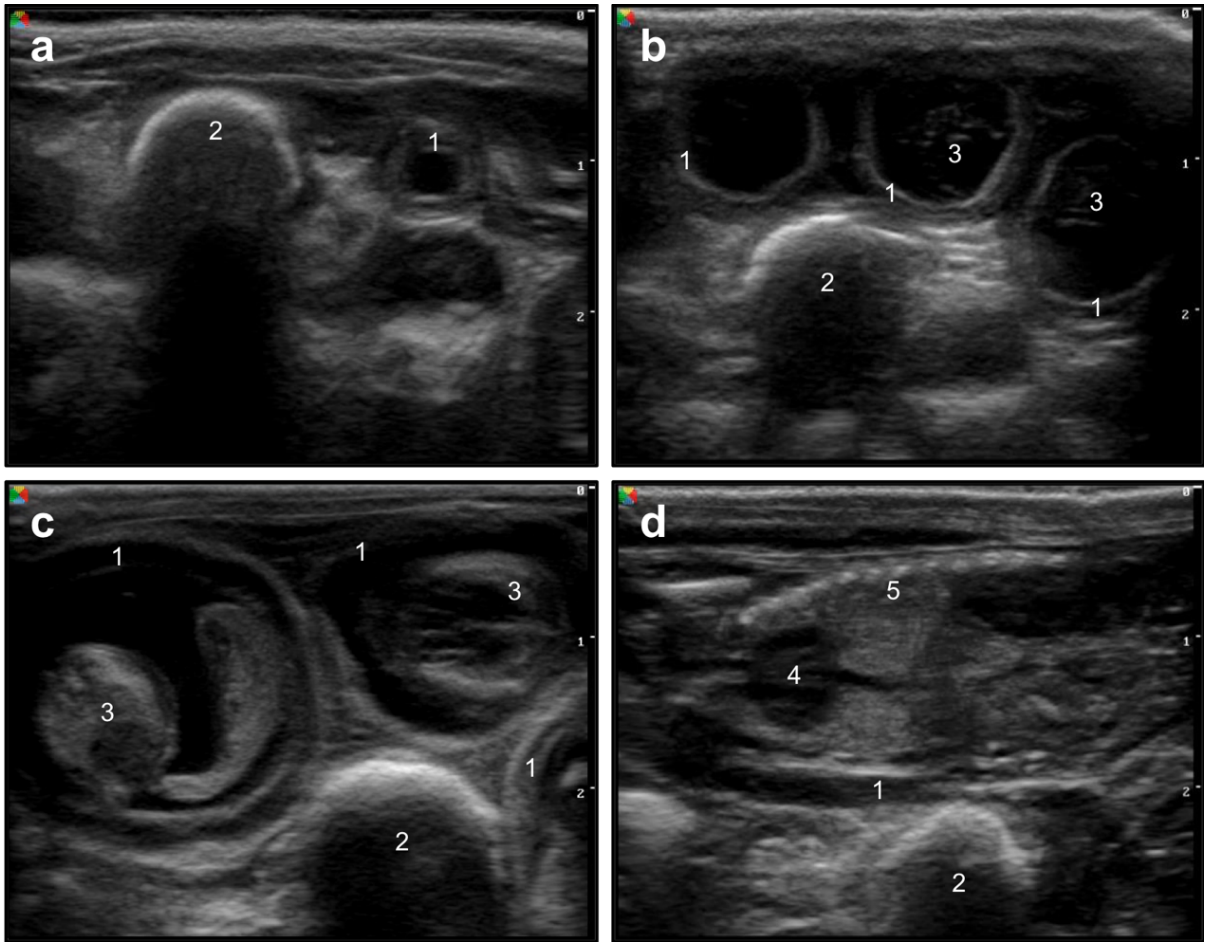
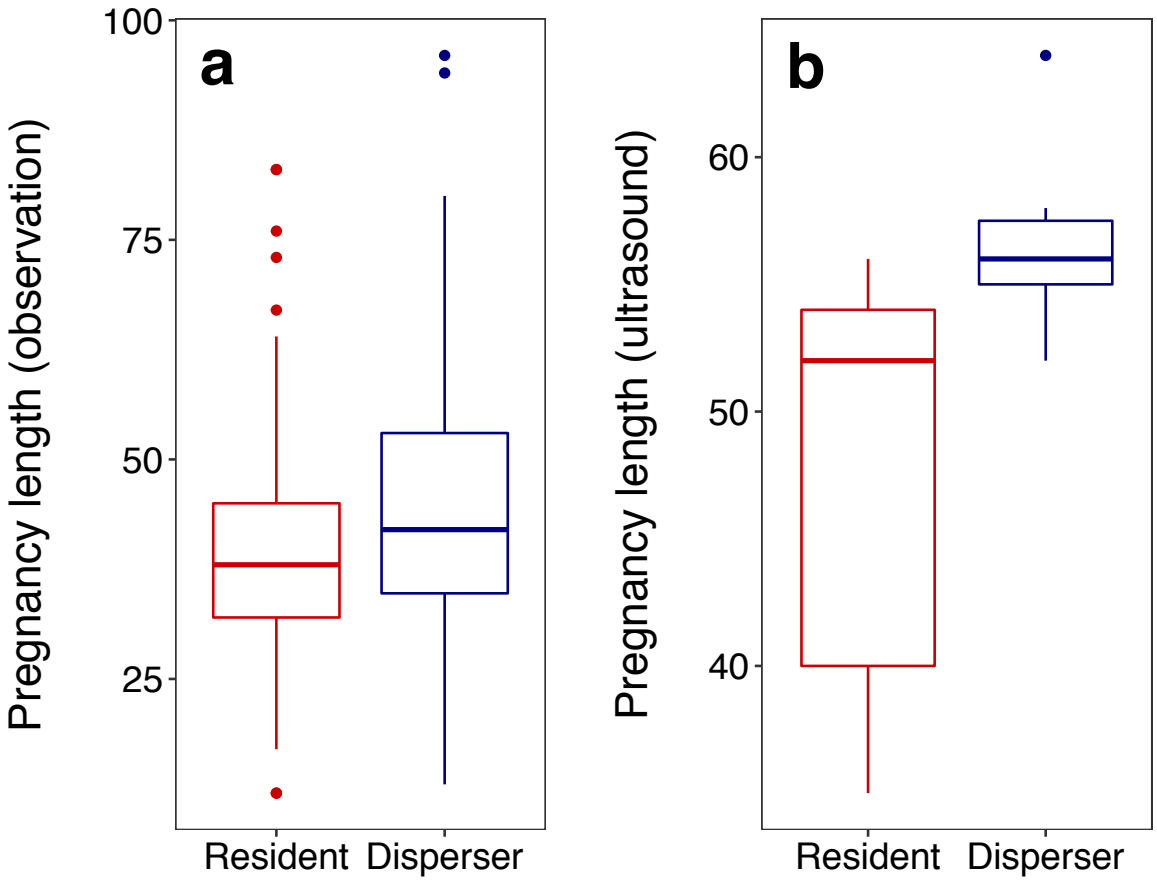


**Figure 4 | Variation in gestation length between resident and dispersing meerkats. a**, Days between first observed abdominal swelling and in the field and parturition. **b**, Days between implantation date estimate based on ultrasound and parturition.



## METHODS

*Study site and population*

Our study was conducted at the Kalahari Meerkat Project (KMP) located on the Kuruman River Reserve (26° 59' S, 21° 50' E) in South Africa. The region is characterized by low seasonal rainfalls between October and April and large daily and seasonal temperature variations [21]. Rainfall and temperature data were available from an onsite weather station. We collected data from a wild meerkat population between September 2013 and July 2018, during which time we followed the pregnancies of 46 dispersers and 103 residents.

*Radio collars*

We fitted lightweight radio collars (Biotrack Ltd, Wareham, UK: 23 g, ~3.5 % of meerkat weight) to dispersing females immediately after eviction from the natal group and one individual per resident group carried a collar as part of the long-term activities at the KMP. To mount the collars, individuals were sedated using a mixture of isoflurane and oxygen in compliance with the KMP protocol. All necessary permits to handle and tag meerkats were granted to the KMP by the Department of Environment and Nature Conservation of South Africa and the Animal Ethics Committee of the University of Pretoria (permit 'FAUNA 192/2014'). Dispersing and resident individuals were regularly tracked by means of VHF telemetry.

*Weight measures and pregnancy assessment*

Meerkats were habituated to the presence of people (<1 m) and trained to climb onto a portable weighing scale allowing for regular weight measures. We could detect pregnancy onset from approximately 28 days after fertilisation due to a swelling of the abdomen and associated weight gain [23]. We identified parturition from a sudden change in abdominal shape and weight loss. Around parturition, we visited animals every other day and, hence, could estimate birth dates with one day accuracy. Pregnancies are very difficult to observe in wild animals and –

although meerkat pregnancies can be determined with high certainty – we decided to use ultrasound scans as an additional and more accurate measurement to proof prolonged pregnancies.

*Ultrasound scans*

To obtain accurate measurements of post-implantation development duration, we monitored the pregnancies of five disperser and five residents with a portable ultrasound machine in the field (Model S6BW, SonoScape Ltd, Nanshan, China). By providing small amounts of water and egg, animals were trained to hold still and be scanned with an ultrasound probe (Linear array L742, SonoScape Ltd, Nanshan, China) and water based lubricant (Fig. 2). Therefore, the procedure could be executed every 4-7 days without the need for anaesthesia and we obtained image time series of embryonic development from immediately after implantation until parturition (Fig. 3, Extended Data Tab. 2). Where possible, we obtained negative scans (i.e., image without embryos) a few days prior to implantation (Extended Data Tab. 1) to narrow down implantation date. We only considered successful pregnancies where pups survived. This could be guaranteed by observing lactation marks on the mother and other group members that helped with nursing immediately after birth. In addition, we observed the pups emerging from the burrow approximately 30 days after parturition. Where more than one female gave birth simultaneously, we collected tissue samples from pups for maternity analysis, which was provided by the KMP [20]. The latter enabled us to ensure that the here described pregnancies all had a successful outcome.

We used the cross-sectional area of each amniotic sac surrounding the embryo from the ultrasound images as an estimate of embryo size (Fig. 3). We drew a circle around the amniotic sac membrane to calculate the area using the software Image J [27] (Extended Date Fig. 1). To define the time of implantation for any pregnancy, we used four pregnancies (i.e., two dispersers and two residents) for which embryo size on the day of the first positive scan was almost identical and very small (~0.45 $cm^2$, Extended Data Tab. 1). From these four

pregnancies we obtained an average embryo development curve, which was linear during the first 40 days (Extended Data Fig. 2a). Using this linear function, we backdated the implantation date from the day of first scanning for all ten pregnancies (Extended Data Fig. 2b). Although implantation must have occurred earlier than our estimate [9,16,17], our method provides a standardised time point to calculate post-implantation development time and hereafter we refer to this point as implantation date.

We observed two additional pregnancies during the captures of two dispersing females under anaesthesia (Extended Data Tab. 1). By touching the animals' abdomen, we could identify the embryo palps and confirm the pregnancies previously observed by visual assessment. The identification of the embryos was done in collaboration with a veterinarian who was present at the captures (S. Patterson, Royal Veterinary College, University of London, UK). We estimated the size of the embryo (i.e., diameter of the amniotic sac) to be approximately 1 cm at the time of palpation (it would be unlikely to detect palps smaller than this size) and backdated the time of implantation with the above described method. Embryos may have been larger at the time of palpation, but we wanted to use a conservative measure to avoid overestimation of pregnancy length. Between the implantation and successful parturition of these two pregnancies we observed a constant increase in maternal weight. Furthermore, the time period would not have been long enough to abort the current pregnancy and conceive and terminate a second successful pregnancy [23]. Thus, for the below described analysis we used ten pregnancies determined by ultrasound and two pregnancies identified during captures.

*Statistical analysis*

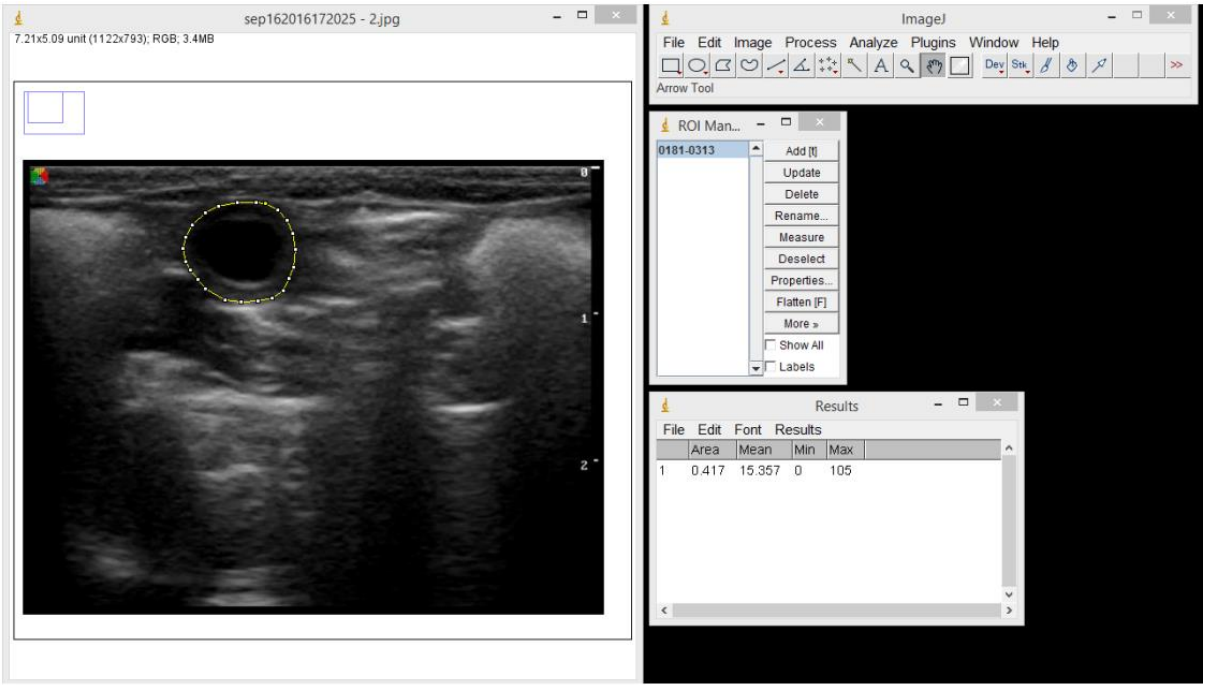
To investigate the influence of dispersal on post-implantation development time based on visual assessment in the field, we first calculated the time between first abdominal swelling and parturition for each pregnancy. We then used a linear mixed effects model in the R [28] library *lme4* [29] with log-transformed embryonic development time as response (right-skewed distribution) to test the difference between dispersers and residents by using a categorical

variable with two factor levels. To control for repeated sampling across individuals, we used individual identity nested in natal group identity as a random intercept term.

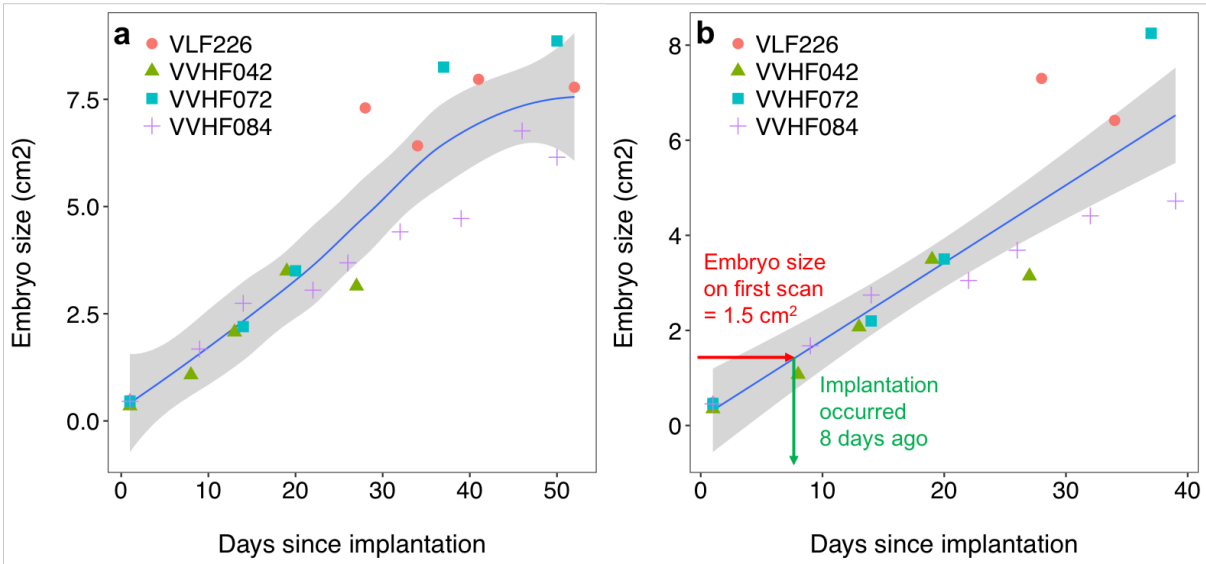
To investigate the influence of dispersal on development time of the ten pregnancies measured with ultrasound, we used the time between estimated implantation date and parturition as response variable. Here, we used a linear model in the basic R environment to test the difference between dispersers and residents. All pregnancies were from different individuals originating from six different natal groups, and we did not use random terms to avoid overfitting of the models.

## EXTENDED DATA

**Extended Data Figure 1 | Embryo cross-section measurement in Image J.** The circle marks the amniotic sac membrane from which we calculated the cross-section area. We used the average size across embryos on a given date if we observed more than one embryo in a female. Average embryo size estimates for each measurement date are given in Extended Data Tab. 2.



**Extended Data Figure 2 | Estimation of implantation date.** To define a standardized embryo-development curve, we used four pregnancies (i.e. two dispersers: VLF226, VVHF072; and two residents: VVHF042, VVHF084) for which embryo size on the day of the first positive scan was almost identical and very small (~0.45 $cm^2$, Extended Data Tab. 1). The obtained development curve was linear during the first 40 days (**a**) and we derived a linear function for these 40 days (**b**). Using this function, we backdated the implantation date from the day of first scanning for all ten pregnancies as shown in the example below (**b**). We only used pregnancies for which the first-scan embryo size was <1.5 $cm^2$ when embryos are still spherical to reduce noise arising from different angles of the scan cross-section.



**Extended Data Table 1 | Pregnancy lengths derived from ultrasound scans.** Two pregnancies were identified by touching the abdomen during captures: Detection method = Capture. In a few pregnancies we obtained negative ultrasound scans a few days prior to implantation to show that embryo development did not start before the estimated date. We estimated implantation date based on embryo size recorded during the first positive scan (see Extended Data Fig. 2). Females used to set up a standardized embryo-development curve are marked with bold font. We identified parturition date by a sudden drop in maternal body mass and change of abdominal shape. All pregnancies shown here produced life offspring.

| | Individual | Detection method | Negative scan | First scan | Embryo size first scan ($cm^2$) | Implantation date | Parturition date | Pregnancy length (days) |
|---|---|---|---|---|---|---|---|---|
| Disperser | VDF162 | Capture | NA | 2014-09-15 | 1.00 | 2014-09-09 | 2014-11-06 | 58 |
| | VDF163 | Capture | NA | 2014-09-15 | 1.00 | 2014-09-09 | 2014-11-12 | 64 |
| | **VVHF072** | Ultrasound | 2016-02-18 | 2016-02-22 | **0.46** | 2016-02-20 | 2016-04-17 | 57 |
| | VBBF104 | Ultrasound | NA | 2016-09-08 | 1.32 | 2016-09-01 | 2016-10-23 | 52 |
| | VJXF080 | Ultrasound | 2016-11-21 | 2016-11-30 | 0.77 | 2016-11-26 | 2017-01-20 | 55 |
| | VBBF109 | Ultrasound | 2017-01-08 | 2017-01-12 | 0.17 | 2017-01-12 | 2017-03-08 | 55 |
| | **VLF226** | Ultrasound | NA | 2018-04-25 | **0.48** | 2018-04-23 | 2018-06-18 | 56 |
| Resident | VPAF038 | Ultrasound | NA | 2016-08-19 | 0.62 | 2016-08-16 | 2016-09-20 | 35 |
| | VPAF037 | Ultrasound | NA | 2016-08-19 | 0.40 | 2016-08-18 | 2016-09-27 | 40 |
| | **VVHF084** | Ultrasound | NA | 2016-09-16 | **0.46** | 2016-09-14 | 2016-11-07 | 54 |
| | **VVHF042** | Ultrasound | 2016-10-17 | 2016-10-24 | **0.50** | 2016-10-22 | 2016-12-13 | 52 |
| | VVHF100 | Ultrasound | NA | 2017-11-18 | 0.60 | 2017-11-15 | 2018-01-10 | 56 |

**Extended Data Table 2 | Embryo sizes during post-implantation development.** We show the average embryo size estimate for each measurement date (see Extended Data Fig. 1 for detailed description of size estimation). The image and video file names refer to the image frames used for cross-sectional area measurements and the ultrasound video footage of each scan. All files can be found in the Supplementary information (SI video files, SI image files).

| | Ind. | Scan date | Days since implant. | Embryo area ($cm^2$) | Image & Video |
|---|---|---|---|---|---|
| Disperser | VVHF072 | 2016-01-18 | -2 | Negative | feb182016070339; feb182016070410 |
| | | 2016-02-22 | 2 | 0.46 | feb222016071958; feb222016072120 |
| | | 2016-03-06 | 15 | 2.20 | mar062016070325; mar062016070421 |
| | | 2016-03-12 | 21 | 3.50 | mar122016091035; mar122016091115 |
| | | 2016-03-29 | 38 | 8.25 | mar292016180845; mar292016180942; mar292016181100 |
| | | 2016-04-11 | 51 | 8.86 | apr112016172415; apr112016172501 |
| | VBBF104 | 2016-09-08 | 7 | 1.32 | sep082016100242; sep082016100420 |
| | | 2016-09-13 | 12 | 2.15 | sep132016080106; sep132016080409; sep132016080533; sep132016080600 |
| | | 2016-09-19 | 18 | 1.79 | sep192016081012 |
| | | 2016-09-24 | 23 | 4.48 | sep242016073735; sep242016073808 |
| | | 2016-09-30 | 29 | 5.61 | sep302016070633; sep302016070742 |
| | | 2016-10-06 | 35 | 4.67 | oct062016070817; oct062016070845 |
| | | 2016-10-15 | 44 | 7.09 | oct152016073910; oct152016073952 |
| | | 2016-10-21 | 50 | 6.91 | oct212016065828; oct212016065922 |
| | VJXF080 | 2016-11-21 | -5 | Negative | nov212016175331 |
| | | 2016-11-30 | 4 | 0.77 | nov302016181905; nov302016182459 |
| | | 2016-12-05 | 9 | 1.49 | dec052016191821; dec052016191858 |
| | | 2016-12-10 | 14 | 2.85 | dec102016184109 |
| | | 2016-12-16 | 20 | 3.28 | dec162016185447; dec162016185514 |
| | | 2016-12-22 | 26 | 4.53 | dec222016181912; dec222016181939 |
| | | 2016-12-28 | 32 | 5.12 | dec282016184311; dec282016184402; dec282016184420 |
| | VBBF109 | 2017-01-08 | -4 | Negative | jan082017065119; jan082017065137 |
| | | 2017-01-12 | 0 | 0.17 | jan122017072738; jan122017072813; jan122017072836 |
| | | 2017-01-14 | 2 | 0.33 | jan142017074117; jan142017074152; jan142017074231; jan142017074342 |
| | | 2017-01-17 | 5 | 0.51 | jan172017070253 |
| | | 2017-01-23 | 11 | 1.20 | jan232017073056; jan232017073124 |
| | | 2017-01-27 | 15 | 1.88 | jan272017070038; jan272017070058; jan272017070133 |

| | | | | | |
|---|---|---|---|---|---|
| | | 2017-01-31 | 19 | 2.80 | jan312017070656; jan312017070721 |
| | | 2017-02-04 | 23 | 4.47 | feb042017081811; feb042017081831 |
| | | 2017-02-09 | 28 | 5.62 | feb092017065254; feb092017065511 |
| | | 2017-02-16 | 35 | 5.25 | feb162017093112; feb162017093130 |
| | | 2017-02-20 | 39 | 6.21 | feb202017090140; feb202017090202 |
| | | 2017-02-25 | 44 | 6.71 | feb252017072653; feb252017072731 |
| | | 2017-03-02 | 49 | 5.80 | mar022017073352; mar022017073419; mar022017073544 |
| | | 2017-03-04 | 51 | 7.38 | mar042017095205; mar042017095304 |
| | | 2017-03-05 | 52 | 4.53 | mar052017080745; mar052017080911 |
| | | 2017-03-07 | 54 | 6.47 | mar072017072230 |
| | VLF226 | 2018-04-25 | 2 | 0.48 | apr252018095412; apr252018095450 |
| | | 2018-05-22 | 29 | 7.30 | may222018084917; may222018085029 |
| | | 2018-05-28 | 35 | 6.42 | may282018090444; may282018090508; may282018090606 |
| | | 2018-06-04 | 42 | 7.97 | jun042018084629; jun042018084703 |
| | | 2018-06-15 | 53 | 7.78 | jun152018084304; jun152018084351 |
| Resident | VPAF038 | 2016-08-19 | 3 | 0.62 | aug192016083810 |
| | | 2016-09-02 | 17 | 6.12 | sep022016082716; sep022016083055 |
| | | 2016-09-12 | 27 | 8.53 | sep122016084351; sep122016084503 |
| | VPAF037 | 2016-08-19 | 1 | 0.40 | aug192016083945; aug192016084031 |
| | | 2016-09-02 | 15 | 2.26 | sep022016082502; sep022016082625 |
| | | 2016-09-12 | 25 | 5.07 | sep122016084036; sep122016084139 |
| | VVHF084 | 2016-09-16 | 2 | 0.46 | sep162016172025; sep162016172121 |
| | | 2016-09-24 | 10 | 1.68 | sep242016181149 |
| | | 2016-09-29 | 15 | 2.74 | sep292016180008; sep292016180110; sep292016180150 |
| | | 2016-10-07 | 23 | 3.05 | oct072016170159; oct072016170235 |
| | | 2016-10-11 | 27 | 3.69 | oct112016180133; oct112016180148 |
| | | 2016-10-17 | 33 | 4.41 | oct172016172526; oct172016172548 |
| | | 2016-10-24 | 40 | 4.72 | oct242016172235; oct242016172302 |
| | | 2016-10-31 | 47 | 6.76 | oct312016173347; oct312016173429 |
| | | 2016-11-04 | 51 | 6.15 | nov042016175533 |
| | VVHF042 | 2016-10-17 | -5 | Negative | oct172016172735 |
| | | 2016-10-24 | 2 | 0.50 | oct242016171023; oct242016171039 |
| | | 2016-10-31 | 9 | 1.25 | oct312016173211 |
| | | 2016-11-04 | 13 | 1.99 | nov042016175228 |
| | | 2016-11-08 | 17 | 2.83 | nov082016172135 |
| | | 2016-11-14 | 23 | 3.53 | nov142016175211 |
| | | 2016-11-19 | 28 | 5.16 | nov192016180720; nov192016180737 |
| | | 2016-11-29 | 38 | 5.65 | nov292016172819 |
| | | 2016-12-03 | 42 | 6.42 | dec032016173941; dec032016173957 |
| | | 2016-12-08 | 47 | 9.39 | dec082016181946; dec082016182007 |

| | | | | | |
|---|---|---|---|---|---|
| | | 2016-12-12 | 51 | 10.85 | dec122016180451; dec122016180614 |
| | VVHF100 | 2017-11-18 | 3 | 0.60 | nov182017063335; nov182017063531; nov182017063559 |
| | | 2017-11-20 | 5 | 0.63 | nov202017174441; nov202017174658; nov202017174709 |
| | | 2017-11-30 | 15 | 2.74 | nov302017101716; nov302017101853 |
| | | 2017-12-04 | 19 | 3.65 | dec042017080629; dec042017080825; dec042017080910 |
| | | 2017-12-27 | 42 | 3.22 | dec272017091336; dec272017091400 |
| | | 2018-01-05 | 51 | 6.73 | jan052018183318; jan052018183356; jan052018183453; jan052018183526 |

## SUPPLEMENTARY INFORMATION

**SI Video files | Ultrasound footage of all pregnancies.** On each observation date, we recorded 1-4 ultrasound video scans of 10 seconds duration of each female. Folders contain one pregnancy each and are labelled with female identity referring to identities in Extended Data Tab. 1. Subfolders are labelled with observation dates and contain all footage recorded on a given date. Names of the footage files refer to the names given in Extended Data Tab. 2. For each file we provide a WMV file that can be played in standard software, and a higher quality CIN file that can only be played on SonoScape ultrasound machines (SonoScape Ltd, Nanshan, China).

**SI Image files | Picture frames with cross-sections of embryos.** From each video footage we used several picture frames to calculate the average cross-sectional area of all embryos that were clearly visible. Folders contain one pregnancy each and are labelled with female identity referring to identities in Extended Data Tab. 1. Subfolders are labelled with observation dates and contain all picture frames obtained from the videos that are provided in SI Video files.

Requests for electronic supplementary materials can be addressed to Nino Maag.

# CHAPTER SEVEN

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## General Discussion

# GENERAL DISCUSSION

Dispersal is an important process governing the dynamics of spatially and socially structured populations. This is because these populations depend on enough individuals that form new groups and reproduce to maintain gene flow and recolonise empty territories. Although we appreciate the importance of the dispersal process, we lack a firm empirical understanding of the underlying mechanisms and how dispersal affects the overall population dynamics. This knowledge gap is due to the technical and logistical difficulties of following wide-ranging individuals in their natural habitat. However, if we want to understand how dispersers affect the overall dynamics of wildlife populations, we need to improve our effort to pursue these individuals and collect long-term survival and reproductive data.

The aim of my thesis was to gain a mechanistic understanding of dispersal and new group formation in a cooperatively breeding species. More specifically, my objectives were to investigate effects of different individual, social, and environmental factors on the dispersal decisions and movement characteristics at each stage of female dispersal; impacts of the constraints associated with dispersal on individual body condition and behaviour; and influence of the conditions and decisions made during dispersal on the long-term demography of newly settled disperser groups. I achieved these objectives by GPS-collaring wild dispersing meerkats, tracking them through unfamiliar landscape over long distances, and collecting high-resolution movement and life-history data for up to three years after settlement. Here, I discuss the entire dispersal process of meerkats in chronological order – from emigration until after settlement – and relate my findings to the current state of knowledge. I point out the main contributions of my thesis to the understanding of cooperative breeder life-history strategies and to dispersal ecology in general. Where appropriate, I combine some of the chapters' results to evoke a coherent understanding of the whole dispersal process.

**Emigration from the natal group**

Nonlinear relationships between population density and emigration are expected where individuals emigrate at low population densities to avoid Alee effects (e.g., inbreeding, lack of breeding partners, Allee et al. 1949), remain in the natal area when densities increase and mates become more abundant, and disperse at very high densities when competition for resources intensifies (Loe et al. 2009, Shaw and Kokko 2014). A nonlinear relationship between population density and emigration is somehow unexpected for meerkats, as previous work has shown a positive relationship between emigration and natal group size (Bateman et al. 2013, Ozgul et al. 2014). My findings are, however, in line with general predictions for cooperative birds and mammals, proposing that subordinate helpers should leave their natal group if local density at home – and thus the benefits of cooperation – decrease (Kokko and Lundberg 2001, Matthysen 2005, Hoogland 2013); at medium densities, when cooperative benefits outweigh the costs of kin competition, subordinates are reluctant to engage in the costly endeavour of dispersal (Courchamp et al. 1999, Clutton-Brock 2002); and when population density becomes very high, the detrimental effects of kin competition will be stronger than the advantages of living in a group and subordinates disperse (Hamilton and May 1977, Moore et al. 2006, Cote et al. 2007).

In addition, densities outside of the natal area can influence dispersal, with higher chances of successful dispersal at low densities, as aggression from local residents is lower and habitat availability higher (Lambin et al. 2001, Morton et al. 2018). I can confirm this with the finding that dispersal time – i.e., time until suitable habitat for settlement is found – increases with population density. However, the fact that settlement rates increase again at highest densities suggests that the effect of kin competition at home is stronger than the costs of settling in high-density environments. As such, my findings on specific density effects during transience and settlement highlight the importance of distinguishing between dispersal stages when investigating individual dispersal decisions. Although inverse density effects have been

suggested to be prominent in social species, my study is one among few to show this in a wild population and the first to describe it throughout the whole dispersal process.

**Costs of dispersal during transience**

The main body of dispersal literature has focused on the drivers that influence emigration, and less is known about the subsequent transient and settlement stages of dispersal (Clobert et al. 2012). This can be explained partly by the fact that it is difficult to collect data on dispersers, but also because conditions at the natal patch are indeed very important drivers of dispersal (e.g., resource competition, inbreeding avoidance). Although within-group processes before emigration seem to be decisive for dispersal in meerkats (Clutton-Brock et al. 2008, Ozgul et al. 2014), my study shows that events occurring after emigration can add significantly to the effects of within-group processes. For instance, individual stress hormone output increases when females move from the emigration to the transient stage, which may be explained by unfamiliarity with the new habitat, predation pressure, or aggression from local resident groups (Pinter-Wollman et al. 2009, Bonte et al. 2012). Similar changes in individual body condition have previously been shown in prospecting individuals of both birds and mammals (Larsen and Boutin 1994, Young et al. 2005, 2006, Ridley et al. 2008, Young and Monfort 2009). However, such changes have never been formally tested for the entire dispersal event. While increased glucocorticoid levels as response to homeostatic challenges – such as social and environmental changes during dispersal – are at first place adaptive (McEwen and Wingfield 2003), elevated stress levels over prolonged periods can have deleterious impacts on an individual's fitness (Wingfield et al. 1998). Hence, if individuals are unable to find suitable territory for settlement in time, chronic stress may lead to decreased fitness later in life (Creel et al. 2013).

In contrast to increased stress levels during dispersal, daily growth rates – although lower in successful dispersers than in residents or returners – do not significantly decrease over the course of the dispersal process. The rather low decrease in body mass is unexpected since a

considerable amount of literature suggests that energetic costs of dispersal are high (reviewed in Bonte et al. 2012). I propose that in cooperative breeders, where subordinates often disperse in multiple-member coalitions and share predator vigilance among multiple individuals (Ligon and Ligon 1978, Packer and Pusey 1982, McNutt 1996, Lundy et al. 1998), dispersers are able to maintain foraging time at a sufficient level. Although I could not show increased growth rates in larger coalitions, my proposition is supported by previous work showing that per capita time spent foraging increases with coalition size, while each coalition member needs to spend less time on vigilance (Young 2004). This could give dispersers of cooperative species a considerable advantage over solitarily dispersing species, especially in harsh environments like the Kalahari Desert, where resources are scarce and predation rates are high. Together with the reproductive advantage of starting a new breeding group with several helpers (Brown et al. 1982, Clutton-Brock et al. 2001), the physiological benefits of dispersing with others could have been a driver in the evolution of cooperative breeding and may explain why arid environments host a majority of the planet's cooperatively breeding species (Lukas and Clutton-Brock 2017).

**Dominance and new group establishment**

In addition to the physiological benefits during transience, coalition size may affect the degree to which coalition members compete for reproductive opportunities in the new group or influence dispersers' ability to colonise a new territory (Bygott et al. 1979, Bernasconi and Strassmann 1999). Both processes are associated with aggression within and between coalitions, and are likely to influence stress hormone levels and body mass (Sapolsky 1993, Buston 2003). My results suggest that competition among female coalition members depends on coalition size as their stress hormone levels increase with increasing number of females. Glucocorticoid levels of reproductive competitors were shown to increase during times of social instability in other species (Sapolsky 1993, Creel 2001) and such instability is likely to occur during dispersal when individuals establish new breeding groups. As aggression and

reproductive conflict increase with group size in social species (Clutton-Brock et al. 2010, Dantzer et al. 2017), increased reproductive competition in larger coalitions may increase individual stress hormone levels. As individuals of social species have been shown to increase their growth rate to compete for reproductive opportunities (Buston 2003, Heg et al. 2004, Huchard et al. 2016), I also expected between-individual variation in daily body mass change to depend on coalition size. Although I could not show that females in large coalitions have higher growth rates than in small coalitions, I found anecdotal evidence showing that if the same coalition changes in size (i.e., a female joins a coalition), high-ranking females increase their growth rate when more competitors accumulate (N. Maag, *unpublished data*).

The variation in scent marking frequency (i.e., urination and defecation) among dispersal stages and with changing social circumstances further indicates that within- and between-coalition competition can influence dispersing individuals. As circulating sex steroids are filtered from the bloodstream through the kidneys and excreted as metabolites in urine (Moss et al. 2001), increased urination rates may be used to attract the opposite sex and establish a firm bond to become the dominant breeding pair. As urination rates are highest immediately after eviction, when most coalitions are joined by unrelated males, and these rates increase with coalition size, I suggest that competition for dominance among female coalition members may already take place during initial phases of dispersal. During and after settlement, defecation probability of females increases with increasing coalition size, suggesting that larger coalitions are able to signal their presence to secure an exclusive territory, whereas smaller coalitions defecate less, potentially to maintain a low profile. I suggest that the costs and benefits of dispersal in cooperative species largely depend on within- and between-coalition competition, which in turn depends on the size of the coalition. I propose that the optimal balance between reproductive opportunities within the new group and competitive abilities towards other groups is key to a successful settlement process.

**Reduced reproductive skew in new disperser groups**

After settlement in a new territory, coalitions need to maximise their reproductive output to increase the long-term success of the new group (Clutton-Brock 2002). In cooperative species, this may be achieved by dominants making reproductive concessions to the subordinates in the new group, leading to a lower reproductive skew and a higher reproductive output per group (Clutton-Brock 1998). My results support this hypothesis by showing that dispersers who become subordinates in new groups have higher conception and birth rates than their resident counterparts, and that – in the initial stages of group formation – dispersers have higher conception rates per group than residents during the same period. As such, I propose that the increased reproductive rates after settlement can promote fast group augmentation and recolonisation success of empty habitat patches.

My results further provide empirical support for the prediction that dispersers should have higher fitness than philopatrics to compensate for the high risks associated with dispersal (Keller and Reeve 1994, Kokko and Ekman 2002). Due to these high costs, subordinates of cooperative birds and mammals often delay dispersal and gain indirect fitness through raising close kin in the natal group (Hamilton and May 1977, Koenig and Dickinson 2004). To attain direct fitness in the natal group, females depend on rare extra-group matings with incoming males or have to wait in the queue for dominance to take over the breeding position (Young et al. 2007, Huchard et al. 2016). My results show that dispersing females can increase their own reproductive rates even if they do not attain dominance in the new group. Furthermore, the route to inherit the dominant position is faster in new disperser groups than in resident groups because I show that survival of competitors is lower and dominance queues are typically shorter due to smaller group size (Nelson-Flower et al. 2018).

**Improved settlement success through prolonged gestation**

The fact that pregnant dispersing meerkats can prolong their gestation indicates that the high costs of dispersal can induce strong selective pressure on reproduction. As discussed in the previous paragraph, fast group augmentation is important for successful settlement, and delaying parturition until settlement is likely to be part of an adaptive strategy to optimize the formation of a new group. The main drivers of gestational delay seem to be social factors, as aggressive attacks during eviction and the acquisition of an exclusive territory are likely to cause the observed prolongation. This is a unique observation, as in other species with variable gestation length, delays are mostly caused by environmental factors such as temperature or spring conditions (Boyd 1996, Clements et al. 2011). The extent to which meerkats can prolong their post-implantation development (maximum observed 80 %) is similar to some of the bat species showing delayed embryonic development (Fleming 1971, Rasweiler and Badwaik 1997), but shorter than in others (Bradshaw 1962, Heideman 1989). In all these bat species, however, embryonic development was delayed immediately after implantation, which was shown using histological tissue samples as embryos are not yet visible on ultrasound during these early developmental stages (Bradshaw 1962, Fleming 1971, Heideman 1989, Rasweiler and Badwaik 1997). This means that delay in meerkats occurs much later during embryonic development, which is exceptional and could provide a female with significant flexibility to respond to immediate changes in her social and physical environment. Although timing of birth may be more flexible, there are likely to be physiological limitations in the extent to which meerkats can delay embryonic development at such a late stage. This could potentially explain the shorter delays in meerkats compared to bats.

**Conclusions and future directions**

The ultimate goal of studying dispersal should be to assess the contribution of dispersers and new group formation to the overall population dynamics. This is because the dynamics of spatially and socially structured populations depend on both within- and between-group

processes, with dispersal-related processes potentially having a large effect on these dynamics (Bowler and Benton 2005). Although I do not show the population dynamic consequences of female dispersal in my thesis, my results on increased reproductive rates in dispersers indicate that female dispersers can influence regional population dynamics. This is important because the meerkat system resembles a metapopulation with source-sink dynamics (Hanski 1999), where large resident groups may function as sources for large dispersing coalitions that can recolonise extinct habitat patches. While dispersers from large source groups have been shown to augment smaller sink groups through immigration in several social species (Pusey and Packer 1987, Creel and Rabenold 1994, Bateman et al. 2013), information on new group formation is typically absent. In many cooperative species, however, female dispersers are not able to immigrate into existing groups, but must establish new breeding units (Wrangham 1980, Doolan and Macdonald 1996, Clutton-Brock and Lukas 2012). In those species, it is of special interest to investigate the contribution of female dispersers to regional dynamics, but has not been documented because dispersers are difficult to follow (Bowler and Benton 2005). My study is a first step towards a comprehensive understanding of dispersal and group formation in cooperative breeders. To gain a complete understanding of how dispersers affect average population fitness, however, I suggest synthesising and connecting my results with a spatially explicit population viability analysis, ideally using individual-based models. This will be the goal of a joined future project in collaboration with my colleagues, and a challenge for other researcher in the field of dispersal ecology and population dynamics.

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# ACKNOWLEDGEMENTS

First and foremost, I would like to thank my co-supervisor, Gabriele Cozzi, for his guidance throughout my PhD thesis. Thank you for innumerable scientific and non-scientific discussions, for giving me a lot of independence in the organisation of the data collection, for getting me interested in repairing cars and building useful field equipment, for commenting on and improving my manuscripts, and for becoming a really good friend. I would like to thank my supervisor, Arpat Ozgul, for his trust in me setting up the field project in South Africa, for giving me the flexibility to develop new ideas and encouraging them, for many fruitful discussions and comments, and for his generous financial support to achieve the best possible results. Thanks to Marta Manser and Tim Clutton-Brock for being part of my PhD committee, for consultations on scientific questions, and for providing access to research facilities and habituated study animals. I further thank Andrew Bateman and Luca Börger, who were also part of my PhD committee and travelled to Zurich on several occasions to discuss my thesis and support me with scientific and statistical advice.

All the research presented here is based on data collected at the Kalahari Meerkat Project (KMP) in South Africa, and numerous people at the project have been involved to make my PhD possible. First, I want to thank my field assistant, Dave Seager, who established the dispersal field project together with me during the first two years and introduced me to the meerkats. Thank you for teaching me field procedures, for being patient when I failed to understand British humor, for the discussion and suggestion of new ideas, for your hard work and dedication to our project, for sharing a drink every so often, and for your friendship. Several more field assistants invested a lot of effort and dedication to pursue this project: Thank you Peter Clark for taking over a rather opportunistic data collection and making it more structured by establishing protocols; thank you Héctor Ruiz-Villar and Ana Morales-González for taking on the field project independently and allowing me to focus on analysis and writing; thank you

Natasha Harrison and Frances Mullany for leading the project into the next generation; and thank you Luc Le Grand and Louis Bliard for your hard work during the transitioning periods.

I further want to thank the volunteers at the KMP for their invaluable information on female evictions to ensure the success of this project, and the meerkat managers Sky Bischoff-Mattson, Lyndsey Marris, Chris Duncan, Laura Meldrum, and Jacob Brown for their tireless effort during captures and support with other needs. I especially want to thank the field site managers of the Kuruman River Reserve, Tim Vink and David Gaynor, who helped me on innumerable occasions with equipment solutions, scientific advice, and their friendship. I am also very grateful to Nanine Gaynor, Jean-Pierre Betshanger, Hendrik and Alta Kooper, Karel and Anna Jacobs, and Mina Kgobe for supporting my project by tending to non-scientific needs; and to the ranchers Lorraine de Bruin, Pieter Kotze, Johnny Kotze, Kobus Lamprecht, and Jood Cloete for letting me on their lands to follow my study animals. Over the four years that I spent at the KMP, I made a lot of very dear friends: Thank you Dave, Tim, Rita, Ryan, Debbie, Rute, Philippe, Miquel, Pauline, Tanja, Sara, Ana, Héctor, Teja, Robbie, Stuard, Seren, Bruce, Cini, Holly, Ed, Kendra, Kats, Coline, Tess, Jack, Jess, Matt, Ramona, and Nicole for sharing with me this wonderful and unforgettable time in the Kalahari.

There is a large group of people from my research group in Zurich and elsewhere, who gave me support in scientific questions. In particular, I want to thank Maria Paniw for her scientific advice on population dynamics, statistical help, and making me laugh every single day. Tina Cornioley and Mollie Brooks have also provided statistical advice on many occasions and I am grateful for it. Thank you Sam and Koen for brightening my days with your humor and being my cohort buddies. Thanks to Jacqui Moser, Lilian Dutoit, Isabel Schöchli, and Florence Zufferey for performing administrative tasks, and Michel Nakano, Tina Siegenthaler, and Cornelia Carnal for sorting out my computer issues. My time in the Popecol research group at the University of Zurich was fantastic and I enjoyed it tremendously: thank you Popecol members for making it such a great time. Extraction of steroid hormones was done in

collaboration with André and Stefanie Ganswindt from the Mammal Research Institute at the University of Pretoria. Special thanks to Nettie Engelbrecht, who introduced me to their laboratory and extraction methods. Steroid analysis was done by Michael and Andrea Heistermann from the Endocrinology Laboratory at the German Primate Center in Göttingen. I further want to thank Constance Dubuc from University of Cambridge for discussions and advice on sex steroids and the female reproductive cycle of mammals.

The route to a PhD is not always easy and my family and friends have given me the necessary support and stability to find my way again when times were difficult. Thank you Mami and Papi for your continuous support in pursuing my dreams, and Cyrill, Levin, and Regula for always being there and listening to my complaints. Thank you Reto, Miri, Luki, Selina, and Nadine for letting me stay at your place when I returned homeless from my field trips and for being my foundation in Zurich. Thank you Gabri, Giorgia, Chris, Jas, Megan, Paul, Rich, Patrick, and Dialy for your friendship and sharing things that we have in common. Very special thanks to my pre-PhD friends Fabio, Lukas, Kathrin, Ueli, Manu, Reto, Thabea, Sigi, Cami, Bürgi, Sam, Ottavia, Marc, Jacqui, Fipsi, and Raphi for their unconditional friendship and being indulgent for my long periods of absence.

During my field work in the Kalahari I met my partner Selin and she has been my inspiration and soulmate ever since. Thank you Selin for always supporting my ideas, for your motivation, and for listening when I needed it most. Thank you for your big heart and your free spirit, and for setting mine free at times. Thanks for showing me again that there is more to nature than science and for taking me outside to rediscover my true self. Thank you for sharing with me this deep love for nature and showing it to me through your own eyes, so that I could find my way back to how I perceived it at the very beginning, when I was a child.

This thesis would not have been possible without the financial support of the Swiss National Science Foundation through funds granted to Arpat Ozgul (Project CR32I3_159743). The Kalahari Meerkat Project has been supported by the European Research Council through funds granted to Tim Clutton-Brock from University of Cambridge (Research Grant No 294494).

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